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ETHIOPIAN MITES OF THE
GENUS *ANDROLAELAPS*
BERLESE *s. lat.*
(ACARI: MESOSTIGMATA)



W. M. TILL

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BY

W. M. TILL

British Museum (Natural History)



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ETHIOPIAN MITES OF THE GENUS *ANDROLAELAPS* BERLESE *s. lat.* (ACARI: MESOSTIGMATA).

By W. M. TILL

British Museum (Natural History), London

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INTRODUCTION

The earliest species of the genus *Androlaelaps* *s. lat.* (including *Haemolaelaps*) to be recorded from the Ethiopian region are those described by Berlese (1911-1918) and Hirst (1916). Radford (1939-1944) added several more species from this region and Zumpt & Patterson (1950, 1951) provided the first keys to the Ethiopian species of the genera *Androlaelaps* and *Haemolaelaps*. Since then many new species have been described by Zumpt and his co-workers, by Keegan (1956) and by Lavoipierre (1955, 1956). With the increased number of species, the existing keys have been found to be inadequate as they were based largely on superficial characters which are subject to intraspecific variation. It was also suspected that many of the new species might be synonyms of older, imperfectly described species, the types of which had never been thoroughly re-examined. The aim of the present investigation is therefore to give redescriptions of the known species, based wherever possible on type material, to try to evaluate the morphological characters observed in the different species, and to prepare a key to the females. Several new species have been included and a host-parasite list is given.

This investigation has been made possible by grants from the British Museum (Natural History) and from the Wellcome Foundation, London. It is based chiefly on material in the collections of the British Museum (B.M.N.H.) and the South African Institute for Medical Research, Johannesburg (S.A.I.M.R.), the latter collection having been placed at my disposal by Dr. F. Zumpt. Material has also been received from Dr. P. L. G. Benoit, Musée Royal de l'Afrique Centrale, Tervuren, Belgium (M.R.A.C.), Dr. R. Taufflieb, Institut de Recherches Scientifiques au Congo, Brazzaville (I.R.S.C.) and Miss J. B. Walker, East African Veterinary Research Organization, Kenya. Types and other specimens have been lent by Miss M. A. Johnson, Liverpool School of Tropical Medicine, Dr. M. M. J. Lavoipierre,

George Williams Hooper Foundation, California, Dr. C. D. Radford, Manchester, and by the Smithsonian Institute, United States National Museum, Washington.

The work was carried out in the British Museum (Natural History) and I am grateful to the Trustees for providing me with the necessary facilities. My thanks are due to Dr. G. O. Evans for his guidance and many helpful suggestions, and to Dr. J. G. Sheals and Mr. D. Macfarlane for advice and assistance in various ways.

EXTERNAL MORPHOLOGY

Females

GNATHOSOMA (figs. 1-5): The gnathosoma is attached subterminally to the anterior end of the body. It consists of a cylindrical *basis capituli* (*gnathosomal base*) enclosing the pharynx and chelicerae and bearing antero-laterally a pair of segmented pedipalps. The dorsal wall of the *basis capituli* extends anteriorly as a membranous flap known as the *tectum*. In the genus *Androlaelaps* this is a transparent structure more or less rounded anteriorly and without ornamentation. On the ventral surface is a median longitudinal groove, the *deutosternum*, which normally bears six rows of anteriorly directed teeth. The number of teeth in each row varies from one to about six. Anteriorly the ventral wall is produced to form the *hypostome* and its processes, the horn-shaped *corniculi* (*external malae*) and the fimbriated *hypostomal processes* (*internal malae*). In most *Androlaelaps* species the *corniculi* are prominent and well sclerotized (figs. 1 & 3), but in *A. sangsteri* and *A. heliosciuri* they are reduced in size, weakly sclerotized and generally inconspicuous (fig. 4).

The hypostomal processes show a variety of modifications and are sometimes very difficult to see. In most *Androlaelaps* species they are similar to those of *A. murinus* (fig. 1), the ventral processes having the form of a pair of triangular flaps, the outer margins of which are fringed. The depth of the fringe varies in different species and is relatively great in *A. tachyoryctes* (fig. 2). The hypostomal processes are unusually large and pilose in *A. georychi* (fig. 5), whilst in *A. walkerae* both the ventral and dorsal processes are modified to form prominent brush-like structures (fig. 3). In *A. heliosciuri* the inner margins of the processes are fringed (fig. 4).

The ventral surface of the gnathosoma bears four pairs of setae, the anterior rostral (g.s. 1) and the posterior external and internal rostral setae (g.s. 2 and g.s. 3) on the hypostome, and the capitular setae (g.s. 4) on the *basis capituli*. The lengths

FIGS. 1-5. Types of gnathosoma (ventral view) in females of the genus *Androlaelaps* s. lat.

Fig. 1. *Androlaelaps murinus* (Berlese)

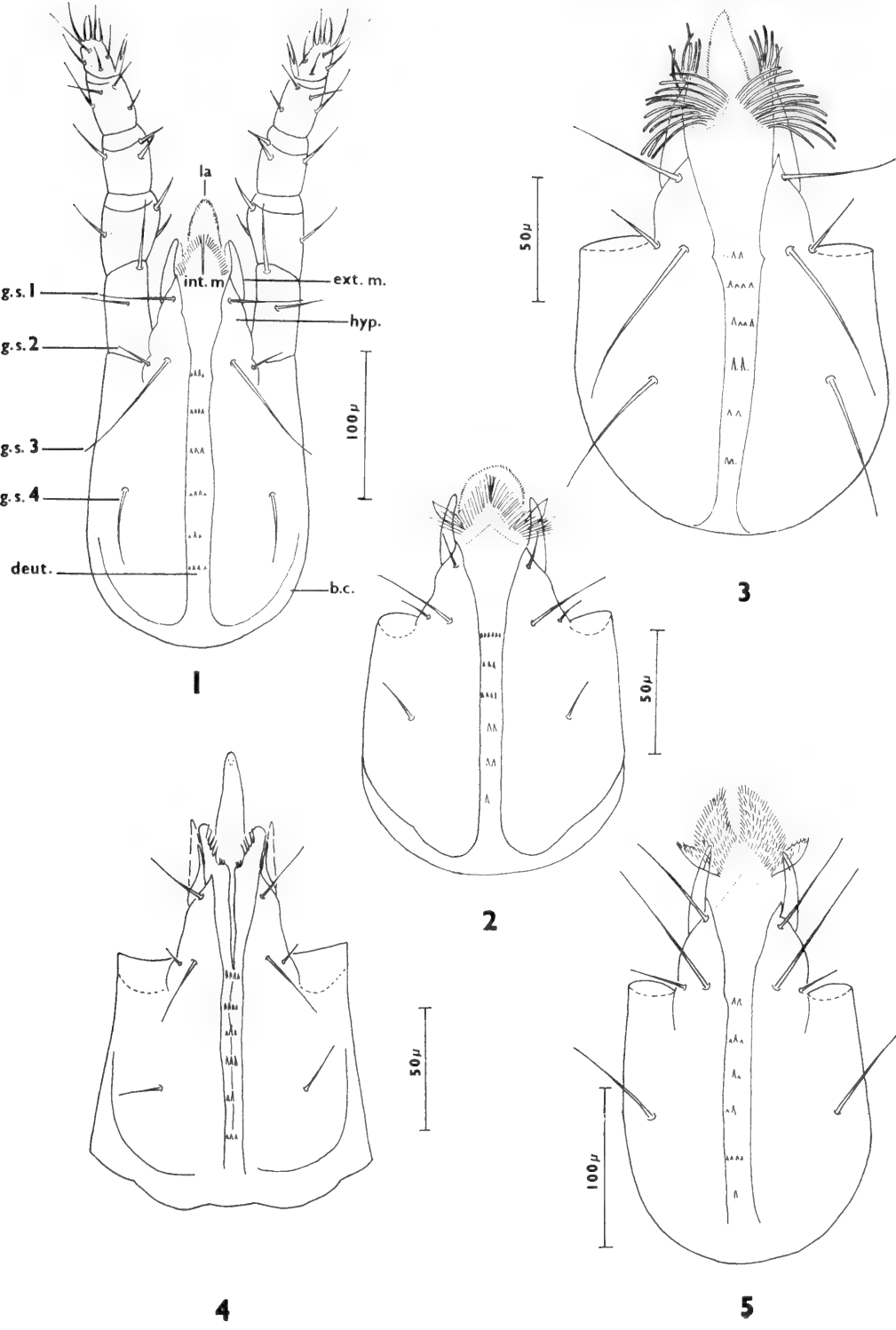
Fig. 2. *Androlaelaps tachyoryctes* (Radford)

Fig. 3. *Androlaelaps walkerae* sp. nov.

Fig. 4. *Androlaelaps heliosciuri* sp. nov.

Fig. 5. *Androlaelaps georychi* sp. nov.

b.c., basis capituli; deut., deutosternum; ext. m., external mala; g.s., gnathosomal seta; hyp., hypostome; int. m., internal mala; la., labrum.



of these setae are relatively constant within the genus. The anterior rostral and capitular setae are usually subequal in length, except in the *scapularis*-group, and the posterior internal rostral seta is 2-3 times as long as the external seta. Lying dorsal to the hypostome and ventral to the chelicerae is a pointed, ciliated structure, the *labrum*.

The *chelicerae* occupy the dorsal region of the gnathosoma. Each terminates in a fixed and a movable digit, both of which are normally dentate and well sclerotized. The fixed digit is usually shorter than the movable one, less strongly dentate, and bears a transparent, seta-like structure, the *pilus dentilis*, the form of which varies in different species. The structure of the chelicerae is peculiar in the *scapularis*-group, in that the movable digit is edentate, except for the terminal hook and at the most one rather blunt subterminal tooth, and bears an additional cutting process provided with large, outwardly directed teeth. The fixed digit is reduced, weakly sclerotized, and bears a flagellar pilus dentilis (fig. 170). In the majority of the *Androlaelaps* species the pilus dentilis is inflated distal to the point of insertion (subgenus *Ischnolaelaps* sensu Fonseca), while in a few, for example *A. hystrici*, *A. phoeniculi*, *A. casalis*, *A. walkerae*, it is slightly inflated near its point of insertion, tapering progressively to a point (subgenus *Atricholaelaps* sensu Fonseca).

On the ventral surface of the chelicera, at the base of the movable digit, is a semicircle of arthrodial filaments. In most of the *Androlaelaps* species these are subequal in length or only slightly variable. In *A. heliosciuri* (fig. 81) two of the filaments are considerably longer than the others, and in *A. murinus* (fig. 109), and *A. zumpti* (fig. 195) there is one filament which is strikingly longer and thicker than the others. The arthrodial membrane between the chelae appears to form an extension which is usually a small, rounded, transparent flap, but which, in *A. zumpti*, is greatly elongated, extending to the tips of the chelae.

The *pedipalps* are 5-segmented; the first free segment, or trochanter, bears 2 setae, the femur bears 5, the genu 6 and the tibia 14 setae. The tarsus, in addition to a number of simple setae, bears a two-tined seta-like structure at its base.

IDIOSOMA: The idiosoma is usually ovoid in shape with no sharp demarcation between the dorsal and ventral surfaces. Almost the entire dorsum is covered by a single scutum which usually has reticular markings and in some species, e.g. those of the *scapularis*-group, may also have a granular appearance. The chaetotaxy of the dorsal shield follows the basic pattern described by Costa (1961, fig. 1) for the genus *Haemolaelaps*. Most of the species have the pattern comprising 39 pairs of setae, although in some species, for example those of the *mesopicos*-group, one or more of the marginal pairs may be situated on the adjacent integument and seta *px3* may be lost. *A. longipes* has an additional pair of setae (*px1*) on the posterior part of the plate (fig. 93), whilst *A. centrocarpus* and *A. hirsti* have extra pairs of setae (*ax* and *px1*) on both the anterior and posterior parts of the shield. Many species show some degree of hypertrichy, a variable number of unpaired, accessory setae developing on the median part of the plate between the "J" series. In *A. taterae* and *A. villosissimus* the dorsal shield has a dense covering of setae which completely obscures the basic pattern. An intermediate condition occurs in

A. walkerae in which the basic pattern is partially obscured by the addition of both unpaired and paired setae. The setae vary considerably in length and in the *scapularis*- and *mesopicos*-groups (excluding *A. wilkini*) and in *A. galagus* those on the central part of the shield are reduced to microsetae.

The ventral surface of the idiosoma bears a sternal, a genital and an anal shield, all of which may show some degree of intraspecific variation. The sternal shield is usually broader than long, reticulate in most species but with a granular appearance in mites of the *scapularis*-group, and bears two pairs of pores and three pairs of setae. In most *Androlaelaps* species the sternal setae are more or less subequal in length, the second and third pairs being very slightly longer than the first pair. In *A. arvicanthis*, *A. graingeri*, *A. marshalli* and *A. theseus* the first pair is relatively short, being $\frac{1}{2}$ – $\frac{3}{4}$ as long as the second pair. Metasternal setae are always present. The presternal area also has a reticulate pattern and bears the *tritosternum*, a bipartite structure of uniform appearance throughout the genus. It consists of a short, undivided, basal portion and two ciliated arms, the laciniae.

The genital shield consists of a relatively more strongly sclerotized posterior portion, varying in shape from the slender tapering form seen in *A. capensis* (fig. 20) and *A. tateronis* (fig. 165) to the greatly expanded, flask-shaped form of *A. rhodesiensis* (fig. 128), and a more weakly sclerotized anterior portion which forms a flap covering the genital orifice. The shield usually has a linear or reticulate pattern at least on the posterior portion. This pattern may be very weakly developed, as in the *scapularis*-group, or it may be very clearly defined and extend on to the anterior portion, as in *A. dasymys* (fig. 51). In some mites the shield also has a granular appearance and in all the species it bears only one pair of genital setae.

The anal shield is ovate or triangular, with the apex directed posteriorly, and encloses the anal orifice. It bears a pair of paranal setae and a single postanal seta. The metapodal plates are small sclerotized structures lying posterior to the fourth pair of coxae. The peritreme extends from the stigma, between coxae III and IV, to a point over coxa I, and the peritremal plate extends posterior to the stigma for a distance equal to approximately twice the diameter of the stigma.

The setae arising from the integument of the idiosoma may be simple or barbed and are variable in number, some species being very sparsely and others relatively densely haired, as for instance *A. taterae* and *A. georychi*. The marginal setae are defined as those lying between the dorsal shield and an arbitrary line commencing at the posterior tip of the anal shield and continuing anteriorly on both sides and equidistant from the lateral margin of the body.

The names of the idiosomal shields have been abbreviated and their measurements taken as follows:—

- DL = median length of dorsal shield
- DW = greatest width of dorsal shield
- SL = median length of sternal shield
- SW = width of sternal shield at level of second pair of setae
- GW₁ = greatest width of genital shield
- GW₂ = width of genital shield at level of genital setae

AL = median length of anal shield

AW = greatest width of anal shield.

LEGS: The legs consist of six recognizable segments, namely, the coxa, trochanter, femur, genu, tibia and tarsus, each tarsus terminating in a caruncle with claws. The segments are usually smooth in outline, but in *A. callosus* some of them have prominent, heavily chitinized swellings (fig. 18). Leg II is usually stouter than the other legs and this feature is most pronounced in the *Androlaelaps*-group. The chaetotaxy of the legs follows a basic pattern which is subject to slight variations. The number of setae per segment found in the majority of the *Androlaelaps* species, and which I have taken to be the normal number for this genus, is given in the following table:—

Leg	Coxa	Trochanter	Femur	Genu	Tibia	Tarsus
I . . .	2	6	13	13	13	—
II . . .	2	5	11	11	10	16
III . . .	2	5	6	9	8	16
IV . . .	1	5	6	10	10	16

The number of tarsal setae listed does not include the two fine setae at the tip of the segment.

Variations have been noted in the number of setae on the first and third tibiae and on the third and fourth genua. Tibia I has 14 setae in *A. rhodesiensis* and *A. walkerae*; tibia III has 9 setae in these two species and also in the species of the *mesopicos*-group, in *A. centrocarpus*, *A. hirsti*, *A. longipes*, *A. phoeniculi*, *A. oliffi*, *A. tateronis*, *A. cricetomydis*, *A. congoensis*, *A. taterae* and *A. villosissimus*. The last three species have ten setae on genu III and *A. spatuliformis* has nine setae on genu IV. The setae are variable in form and may be smooth or barbed, hair-like, spine-like, pointed or blunt. In the mites of the *Androlaelaps*-group one of the ventral setae on femur II is modified to form a stout spur-like process.

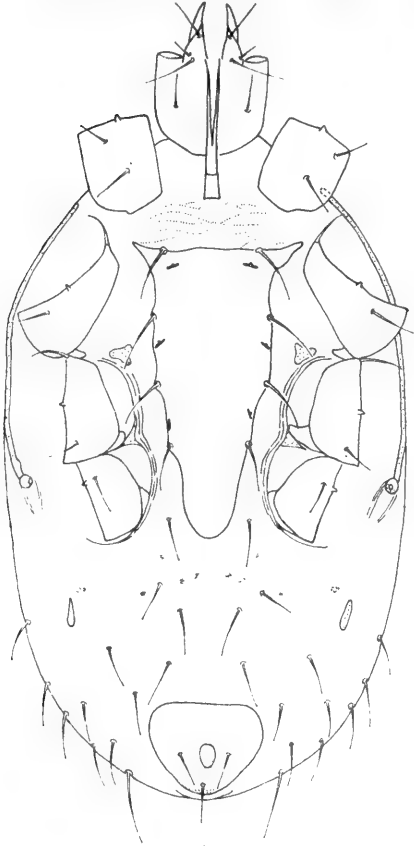
Males

The gnathosoma of the male is similar in structure to that of the female. The chelicera, however, has its movable digit modified to form a spermadactyl which serves as a copulatory organ. This may be relatively short and straight, as in *A. casalis* (fig. 29), *A. hystrici* (fig. 88) and others, or relatively long and coiled as in *A. taterae* (fig. 164), *A. patersoni* (fig. 124) and *A. spreo* (fig. 145). The fixed digit bears a pilus dentilis, sometimes very difficult to detect, which resembles the pilus dentilis of the corresponding female.

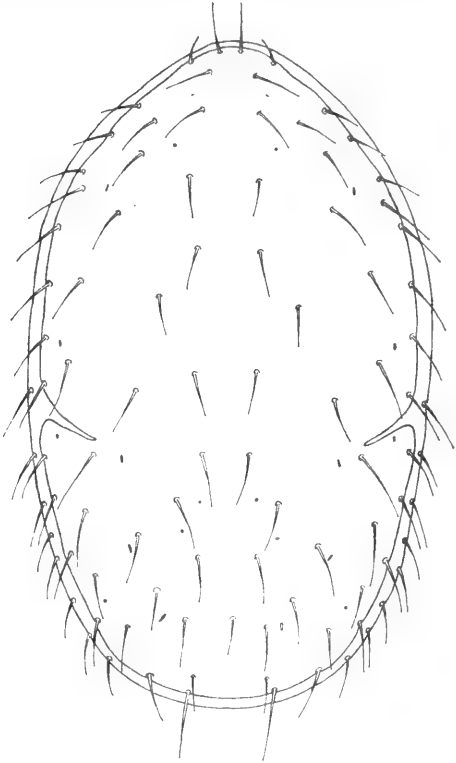
The dorsal shield has the same chaetotactic pattern as in the female, although the setae are often relatively longer.

The ventral shields in most *Androlaelaps* species are fused to form a single holovenral plate which shows varying degrees of expansion behind the fourth pair of legs. The shield bears four pairs of sternal, one pair of genital, and the usual

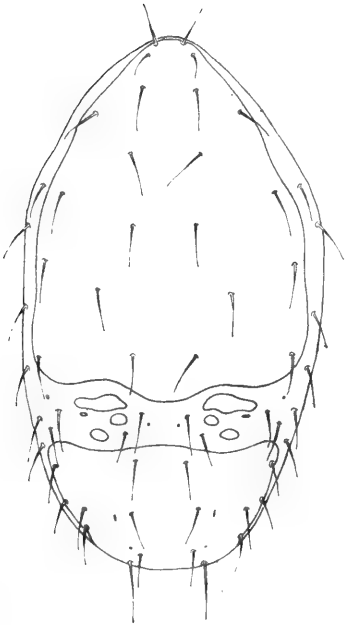
FIGS. 6-9. *Androlaelaps casalis* (Berlese). Venter (Fig. 6) and dorsum (Fig. 7) of deutonymph; dorsum (Fig. 8) and venter (Fig. 9) of protonymph.



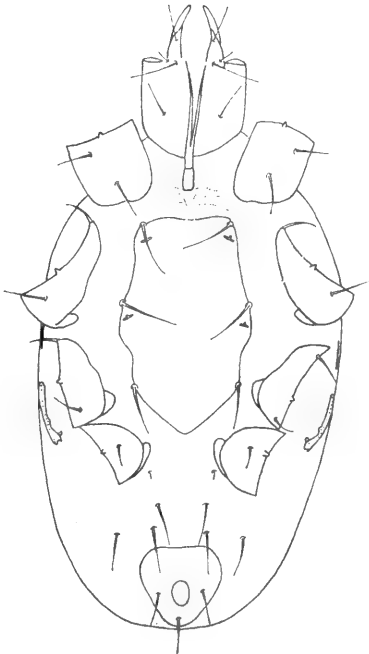
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8



9

three anal setae. The number of setae in the preanal region varies between two or three pairs, in the species with a narrow plate, for example the *mesopicos*-group, and many, in those species with an expanded plate, for instance *A. murinus* and *A. taterae*. The usual number is five pairs.

The anal shield is separated from the sternito-ventral shield in *A. centrocarpus*, *A. hirsti* and *A. longipes* (species with 40 or 41 pairs of setae on the dorsal shield) and also in *A. tauffliebi*. In all species the genital orifice is presternal.

The chaetotaxy of the legs follows the same pattern as in the corresponding females although certain setae, for example in the *mesopicos*-group, may be modified to form thickened spines or spurs.

Immature Stages

According to Bregetova (1956) *Haemolaelaps* females are able to lay eggs with developed larvae or they may give birth to larvae or even to protonymphs. As far as the Ethiopian species are concerned only proto- and deutonymphs have been recorded up to now.

The following description of the nymphal stages is based on specimens of *A. casalis* from deep poultry litter in England. The immature stages of the other species will not be described as so very little material is available.

PROTONYMPH (figs. 8-9): The gnathosoma resembles that of the female except that the palps have not yet acquired their full complement of setae. The trochanter bears one ventral seta, and the femur, genu and tibia bear 4, 5 and 12 setae respectively.

The dorsum has a large anterior podonotal shield bearing eleven pairs of setae, a smaller, posterior, pygidial shield bearing eight pairs of setae, and three pairs of small intermediate platelets or mesonotal scutellae. The sternal shield, which bears three pairs of setae and two pairs of pores, does not extend beyond the middle of coxae IV. The peritremes are short and do not reach beyond coxae III. There is no genital shield or genital orifice.

The legs have not yet acquired their full number of setae, those present being listed in the following table:—

Leg	Coxa	Trochanter	Femur	Genu	Tibia	Tarsus
I . . .	2	4	10	8	8	—
II . . .	2	4	8	6	7	15
III . . .	2	4	5	6	7	15
IV . . .	1	4	4	6	7	15

DEUTONYMPH (figs. 6-7): The deutonymph is larger than the protonymph and the palps and legs have the same number of setae as in the adult stages. The podonotal, mesonotal and pygidial shields have fused to form a single dorsal scutum which has a lateral incision on either side, behind seta *s*₇. The number of setae on the shield is the same as in the adult. On the ventral surface the sternal shield extends to the level of the posterior border of coxa IV. It bears four pairs of setae (the sternals and metasternals) and three pairs of pores. The peritremes are long, reaching coxae I. Metapodal plates are present, and also several small areas of sclerotization on the median part of the venter,

CLASSIFICATION

It has long been recognized that the genera *Androlaelaps* and *Haemolaelaps* are very closely related to one another as well as to the genus *Hypoaspis* Canestrini. Both *Androlaelaps* and *Haemolaelaps* were originally described by Berlese as subgenera of *Laelaps* Koch. Subsequently *Haemolaelaps* (Berlese, 1916) and then also *Androlaelaps* (Vitzthum, 1943; Zumpt, 1950; Zumpt & Patterson, 1950) were placed as subgenera of *Hypoaspis*, and more recently both have been given generic status (Strandtmann, 1949; Zumpt & Patterson, 1951; Keegan, 1956; and others).

There is still some confusion, however, regarding the delimitation of the genus *Haemolaelaps*. The genera *Atricholaelaps* Ewing and *Ischnolaelaps* Fonseca were synonymized with *Haemolaelaps* by Strandtmann (1949), a decision which has been accepted by most other workers on this group. Fonseca (1959), however, recommended that *Haemolaelaps* be kept as a monotypic genus for *H. marsupialis* Berlese, the remaining species being allocated to the genus *Atricholaelaps* with its subgenus *Ischnolaelaps*. He based these divisions on the form of the pilus dentilis, a feature which he himself admits is sometimes difficult to interpret. *Eubrachylaelaps* Ewing (= *Cyclolaelaps* Ewing) and *Zygolaelaps* Tipton were added to the synonymy by Zumpt and his co-workers (1951, 1958). *Cavilaelaps* Fonseca was included in the synonymy by Zumpt & Patterson (1951), but was not listed by Zumpt & Till (1961). Its status is still doubtful as I have not been able to examine the type species. The genus *Turkiella* Zumpt & Till was synonymized with *Androlaelaps* by Keegan (1956).

The genera *Androlaelaps* and *Haemolaelaps* resemble one another very closely in their dorsal and ventral sclerotization and chaetotaxy, in their leg chaetotaxy and in the structure of the chelicerae. In both genera the sternal shield of the female is broader than long, the pilus dentilis is inflated or long and slender, and the digits of the male chelicerae are weakly sclerotized and edentate, the fixed digit being shorter than the movable one. The only differences between *Androlaelaps* and *Haemolaelaps* are that in females of the former genus leg II is relatively more stout and one of the ventral setae on femur II is thickened to form a spur-like structure. These features, however, are not clear-cut. There is a gradation both in the thickness of the second leg and in the nature of its setae from the *Haemolaelaps* to the *Androlaelaps* species. Furthermore, males of the *mesopicos*-group of *Haemolaelaps* species have a stout spur-like seta in the position corresponding to the *Androlaelaps* spur, whilst the females have only a simple seta.

The genus *Hypoaspis* differs from *Androlaelaps* and *Haemolaelaps* in that the length of the sternal shield of the female usually equals or exceeds the breadth; the pilus dentilis is short, slender, scarcely visible, and the digits of the male chelicera are well sclerotized, equal in length, with dentate internal margins. The genus *Gaeolaelaps*¹ Trägårdh, with *Laelaps aculeifer* Canestrini as type species, appears to bear the same relationship to *Hypoaspis* as *Androlaelaps* does to *Haemolaelaps*.

It seems possible that these mites may all have arisen from a common free-living

¹ The genus *Gaeolaelaps* was mentioned in Berlese's note book but was never described. Berlese referred to the genus *Geolaelaps* in 1924 (Redia 15 : 254), but without designating a type. Trägårdh (1952, Ark. Zool. 4 ser. 2 : 66) states that Berlese (in MS) had designated *L. aculeifer* as the type.

Hypoaspis-like ancestor, giving rise on the one hand to species with simple setae on leg II (*Hypoaspis*) and on the other to species having an enlarged second leg with thickened setae (*Gaeolaelaps*). Modified, elongate, edentate male chelae could have developed in the mites of both branches which became adapted to a parasitic mode of life, giving rise to species of the *Haemolaelaps* and *Androlaelaps* types respectively.

In deciding upon the status of these four genera there seemed to be three possibilities:—

1. To give all four generic status.
2. On the basis of leg setae to combine *Haemolaelaps* with *Hypoaspis* and *Gaeolaelaps* with *Androlaelaps*.
3. On the basis of male chelae, female sternal plate and pilus dentilis, to combine *Haemolaelaps* with *Androlaelaps* and *Gaeolaelaps* with *Hypoaspis*.

Of these three propositions the third seems to be the most appropriate and *Haemolaelaps* has consequently been synonymized with *Androlaelaps*. In this connection it is interesting to note that two species described recently (*H. travisi* Delfinado 1961 and *H. vietnamensis* Grochovskaya and Nguyen-Xuan-Hoe 1961) as having the *Androlaelaps* type of leg setation have been allocated to the genus *Haemolaelaps* by their respective authors.

Bregetova (1956), in her diagnosis of the genus *Androlaelaps*, describes the chelicerae as being similar in structure in both sexes, the male having a spermadactyl added parallel to the movable digit. This is the type of chelicera found in males of the genus *Hypoaspis*. However, Berlese's (1887) drawing of *A. hermaphrodita*, the type species of *Androlaelaps*, shows that the male chelae are elongate and edentate. The *Androlaelaps* species described from the Ethiopian region are clearly co-generic with *A. hermaphrodita*, whereas those listed by Bregetova (*A. sardous* Berlese, *A. karawaiiewi* Berlese and *A. pavlovskii* Bregetova) are of the *Hypoaspis* type.

In the key which I have given to the females of the genus *Androlaelaps* s. lat., couplets 2 to 5 refer to the species bearing the modified spur-like seta (*Androlaelaps*-group), whilst the remaining couplets refer to species previously assigned to the genus *Haemolaelaps* (*Haemolaelaps*-group).

On the basis of morphological features, many of the species which I have included in the *Haemolaelaps*-group could be arranged in well-defined sub-groups. *A. cryptomius*, *A. scapularis* and *A. tauffliebi*, three species parasitic on mole-rats, form a distinct group having the movable cheliceral digit in two parts, microsetae on the dorsal shield, and "granular" dorsal and ventral idiosomal shields. The status of these mites may have to be reconsidered and the group regarded either as a subgenus of *Androlaelaps* or even as a distinct genus.

A. taterae and *A. villosissimus* differ from all other *Androlaelaps* species in their dorsal chaetotaxy. *A. centropus*, *A. hirsti* and *A. longipes* form a fairly well-defined group having 40–41 pairs of dorsal setae, nine setae on tibia III and a separate anal shield in the male.

The *mesopicos*-group, comprising four species associated with birds, namely,

A. haydocki, *A. mesopicos*, *A. steyni* and *A. wilkini*, is characterized by the sinuous posterior setae, the position of the first pair of sternal setae on the presternal area and by the presence of nine setae on tibia III.

The *zulu-glasgowi*-group comprises a number of apparently very closely allied species (*A. dasymys s. lat.*, *A. glasgowi*, *A. pachyptilae*, *A. patersoni*, *A. spreo*, *A. suncus* and *A. zulu*) whose status is not quite clear, and it is possible that some of them are no more than subspecies or varieties.

A. glasgowi represents a cosmopolitan species complex which has been recorded from a wide variety of mammalian and bird hosts (Strandtmann, 1949; Bregetova, 1956). According to Bregetova, this species has only 38 pairs of setae on the dorsal shield, setae *s*₃ being absent. This has been confirmed in specimens from Japan and Astrakhan in the collection of the British Museum (Natural History). American specimens which I have been able to examine, namely, the type specimen of *A. glasgowi* (lent by the Smithsonian Institute, Washington) and several specimens from the collection of the South African Institute for Medical Research, have 39 pairs of setae. Mites from Israel (Costa, 1961) and from Southern Africa also have 39 pairs of dorsal setae as well as a number of asymmetrically arranged setae on the posterior part of the dorsal shield. There are also slight morphological differences, chiefly in relative measurements, between mites from different host species (Strandtmann, 1949).

A. zulu very closely resembles *A. glasgowi*, differing from it in having a larger genital shield and longer setae on the dorsal shield. In both species the pilus dentilis is strongly inflated proximally, the terminal portion being slender and recurved. Specimens previously identified by Zumpt & Till (1956) as forms of *A. glasgowi* in which the genital shield is bordered by three pairs of setae would appear to belong to *A. zulu*.

The remaining members of this group differ from *A. glasgowi* and *A. zulu*, and from one another, in the form of the pilus dentilis, the relative lengths of the arthrodial filaments at the base of the movable digit of the chelicera and the dorsal setae, and the relative measurements of parts of the body.

A. dasymys s. lat. is considered to include *A. davis*i and *A. labuschagnei* which appear to differ from *A. dasymys s. str.* only in size, degree of sclerotization and relative setal lengths. *A. dasymys* was based on a single damaged specimen which lacks most of the dorsal setae and of which the pilus dentilis is not clearly visible. By courtesy of Dr. P. L. G. Benoit (Musée Royal de l'Afrique Centrale) three mites from *Rhabdomys pumilio* have been examined which appear to be identical with *A. dasymys* and which are in rather better condition. These mites are relatively large and robust, the dorsal shield measuring 1025–1064 μ by 700–750 μ .

The type series of *A. davis*i consists of rather smaller, less heavily sclerotized mites, in which the dorsal shield measures 822–888 μ by 516–569 μ . Examination of further material from the type host of *A. davis*i shows the dorsal chaetotaxy of this species to be variable in that accessory setae may be present or absent. Mites from different host species show a variation in the relative lengths of the dorsal setae. The type specimens of *A. labuschagnei*, which unfortunately are not in very good condition, appear to be intermediate between *A. davis*i and *A. dasymys s. str.*

9. First pair of sternal setae inserted on anterior margin of sternal shield. Distance between genital and anal shields more than twice distance from anterior margin of anal shield to anterior margin of anus. Dorsal shield almost parallel-sided (figs. 131-132).
A. sangsteri (Radford)
- First pair of sternal setae inserted on presternal area. Distance between genital and anal shields about half the distance from anterior margin of anal shield to anterior margin of anus. Dorsal shield ovoid (figs. 79-80).
A. heliosciuri sp. nov.
10. Dorsal shield with seta *J*₄ at least 5 times as long as seta *J*₁ (fig. 55).
A. galagus (Lavoipierre)
- Dorsal shield with setae *J*₁ and *J*₄ subequal 11
11. Setae *Z*₅ whip-like and sinuous (fig. 102). From birds (*mesopicos*-group) 12
- Setae *Z*₅ normal. From mammals and birds 15
12. Setae *i*₄ and *z*₂ very minute, their lengths about $\frac{1}{4}$ the distance between their bases, or less. Sternal shield granular 13
- Setae *i*₄ and *z*₂ longer, their lengths at least $\frac{1}{2}$ the distance between their bases. Sternal shield reticulate (fig. 182-183) **A. wilkini** (Till)
13. Anterior seta of coxa III thick, spine-like (fig. 148) **A. steyni** (Till)
- Anterior seta of coxa III normal, hair-like 14
14. Marginal setae of posterior half of dorsal shield simple (fig. 102) **A. mesopicos** (Radford)
- Two pairs of marginal setae (*S*₂ and *S*₃) of posterior half of dorsal shield whip-like, sinuous (fig. 78) **A. haydocki** (Till)
15. Some leg segments with pronounced chitinized swellings (fig. 18) . **A. callosus** (Berlese)
- Legs without swellings 16
16. Dorsal shield with seta *p*_{x1} developed (fig. 83) 17
- Dorsal shield with seta *p*_{x1} absent 19
17. Seta *ax* present (figs. 31, 83) 18
- Seta *ax* absent (fig. 93) **A. longipes** (Bregetova)
18. Posterior dorsal shield without or with a few accessory setae restricted to the region *J*₃ to *J*₅ (fig. 83) **A. hirsti** (Keegan)
- Posterior dorsal shield with numerous accessory setae extending anterior to seta *J*₁ (fig. 31).
A. centrocarpus (Berlese)
19. Tibia III with 9 setae 20
- Tibia III with 8 setae 24
20. Genital shield greatly expanded, greatest width at least 1.6 times width at level of genital setae 21
- Genital shield not, or only slightly expanded, greatest width not exceeding 1.3 times width at level of genital setae 23
21. Genu III with 10 setae **A. congoensis** sp. nov.
- Genu III with 9 setae 22
22. Lengths of setae *i*₄ and *z*₂ at least twice the distance between their bases (fig. 129). Tibia I with 14 setae **A. rhodesiensis** (Zpt. & Patt.)
- Lengths of setae *i*₄ and *z*₂ less than half the distance between their bases (fig. 43). Tibia I with 13 setae **A. cricetomydis** sp. nov.
23. Tarsus II terminating in pointed setae only. Lengths of setae *i*₄ and *z*₂ approximately $\frac{1}{4}$, or less, the distance between their bases. Dorsal shield with 37 pairs of setae (fig. 126).
A. phoeniculi (Zumpt & Till)
- Tarsus II with at least one of the terminal setae stout and blunt. Lengths of setae *i*₄ and *z*₂ approximately equal to the distance between their bases. Dorsal shield with 39 pairs of setae (figs. 115, 166) **A. tateronis** (Radford)
- **A. oliffi** (Zumpt & Patterson)
24. Tarsus II with 3 stout, blunt terminal spines (fig. 157) 25
- Tarsus II terminating in pointed setae only 26
25. Sternal shield granular. Caruncle of tarsus IV normal, its length being $1\frac{1}{4}$ times the greatest width of the tarsus **A. tachyoryctes** (Radford)

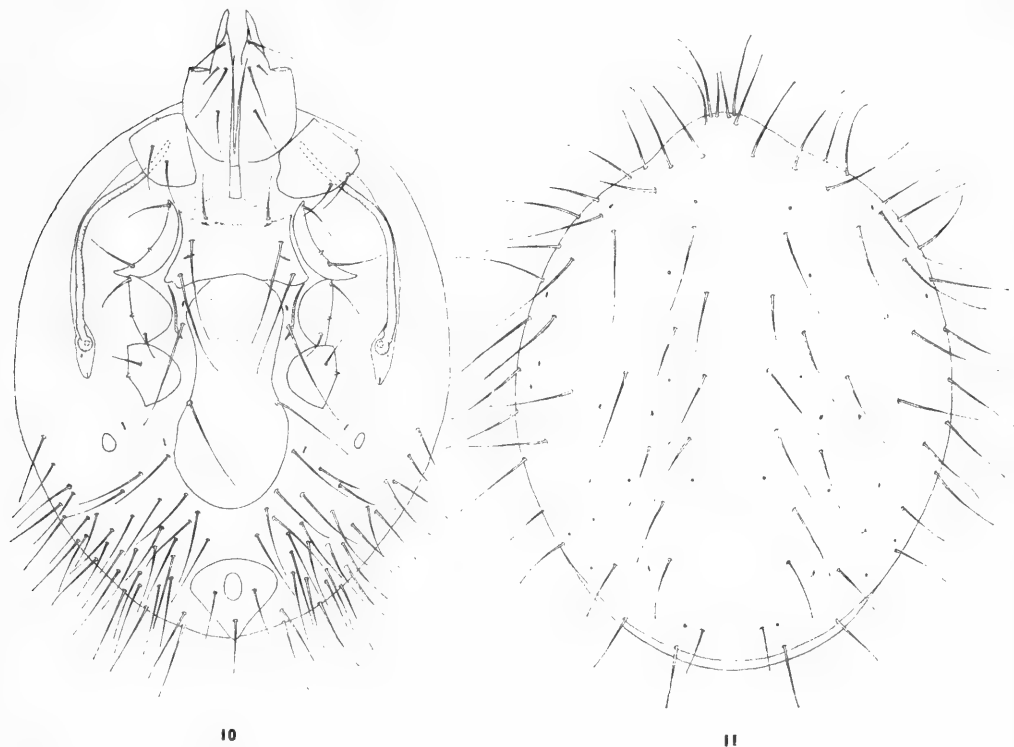
- Sternal shield faintly reticulated. Caruncle of tarsus IV elongated, its length being at least twice the greatest width of the tarsus. **A. capensis** (Hirst)
- 26. Movable digit of chelicera in two parts, one part being dentate; fixed digit of chelicera weakly sclerotized, membranous in appearance (figs. 135, 170). Setae *i4* and *z2* very minute, their lengths not exceeding $\frac{1}{4}$ the distance between their bases (fig. 134). (*scapularis*-group) 27
- Movable digit of chelicera normal; fixed digit normally developed, well sclerotized. Setae *i4* and *z2* relatively longer, their lengths nearly half the distance between their bases, or longer 29
- 27. Genital shield short, widely separated from anal shield (fig. 45) **A. cryptomius** (Radford)
- Genital shield large, flask-shaped, extending almost to anal shield. 28
- 28. Width of sternal shield at most $2\frac{1}{4}$ times its length. Arthrodial filaments at base of movable digit of chelicera subequal in length (figs. 133, 135) **A. scapularis** (Berlese)
- Width of sternal shield 3 times its length. Four or 5 of the arthrodial filaments at the base of the movable digit of the chelicera conspicuously longer and stouter than the others (figs. 168, 170) **A. tauffliebi** sp. nov.
- 29. Genu IV with 9 setae **A. spatuliformis** (Lavoipierre)
- Genu IV with 10 setae 30
- 30. Integument of venter, behind coxae IV, relatively densely haired, about 15 pairs, or more, of truly ventral setae (figs. 59, 107) 31
- Integument of venter relatively sparsely haired, about 10 pairs, or less, of truly ventral setae 32
- 31. Chelicera with arthrodial filaments subequal in length. Pilus dentilis moderately and more or less evenly inflated, elongate (fig. 61). Hypostomal processes very large and hairy (fig. 5) **A. georychi** sp. nov.
- Chelicera with one very long arthrodial filament. Pilus dentilis strongly inflated basally, terminal portion slender, curved (fig. 109). Hypostomal processes normal (fig. 1). **A. murinus** (Berlese)
- 32. Setae on dorsal shield very long and thick; seta *J1* reaches almost to base of *J4*; lengths of setae *i4* and *z2* at least twice the distance between their bases (fig. 63). **A. ghanensis** sp. nov.
- Setae on dorsal shield relatively shorter and more slender; seta *J1* does not reach base of *J3*; lengths of setae *i4* and *z2* less than $1\frac{2}{3}$ the distance between their bases 33
- 33. Pilus dentilis slender (figs. 27, 91) 34
- Pilus dentilis inflated (figs. 187, 195) 35
- 34. Genital shield widest anterior to first pair of flanking setae, then tapering posteriorly. Distance between genital and anal shields more than twice distance from anterior margin of anal shield to anus (fig. 89) **A. hystrici** (Zumpt & Till)
- Genital shield widest at level of second pair of flanking setae, broadly rounded posteriorly. Distance between genital and anal shields not exceeding distance from anterior margin of anal shield to anus (fig. 25) **A. casalis** (Berlese)
- 35. Anal shield $1\frac{1}{2}$ times longer than broad (fig. 193). **A. zumpti** sp. nov.
- Anal shield about as long as broad **zulu-glasgowi** complex
 - a. Parasites of birds b
 - Parasites of mammals d
 - b. Tarsus IV with length to greatest width not greater than 5 : 1. Seta *J1* extends to a point approximately level with base of seta *J2* (fig. 118). **A. pachyptilae** (Zumpt & Till)
 - Tarsus IV with length to greatest width about 7 : 1. Seta *J1* extends well beyond base of *J2*, at least half way to base of *J3* c
 - c. Pilus dentilis spatulate, terminating in a short, slightly bent, sharp point (fig. 122) **A. patersoni** (Zumpt & Till)
 - Pilus dentilis with a larger proximal and a smaller distal inflation, the latter terminating in a very fine point (fig. 143) **A. spreo** (Zumpt & Till)

d. Chelae 50–65 μ long; 2 or 3 of the arthrodial filaments at the base of the movable digit distinctly longer than the others. Pilus dentilis as in fig. 53 **A. dasymys** (Radford)

– Chelae 30–40 μ long; arthrodial filaments at base of movable digit usually subequal in length e

e. Pilus dentilis with distal portion inflated (fig. 153). Tarsus IV with length to greatest width not more than 5 : 1 **A. suncus** sp. nov.

– Pilus dentilis with distal portion slender, usually curved (figs. 67, 187). Tarsus IV with length to greatest width at least 6 : 1 f



FIGS. 10–11. *Androlaelaps arvicantis* Radford, female. Venter (Fig. 10); dorsum (Fig. 11).

f. Setae of dorsal shield relatively short, lengths of *i4* and *z2* at most slightly exceed the distance between their bases. Genital shield bordered by two pairs of setae (figs. 65–66) **A. glasgowi** (Ewing)

– Setae of dorsal shield relatively long, lengths of *i4* and *z2* at least $1\frac{1}{2}$ times the distance between their bases. Genital shield bordered by three pairs of setae (figs. 185–186). **A. zulu** (Berlese)

Androlaelaps arvicantis Radford

Androlaelaps arvicantis Radford, 1944, *Parasitology* 35 : 162, fig. 4.

Turkiella arvicantis, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 225.

Androlaelaps equatoriensis Keegan, 1956, *J. Egypt. publ. Hlth. Ass.* 31 : 230, fig. 15. (*syn nov.*).

FEMALE (figs. 10–13): Deutosternum with 6 rows of teeth, 4 to 5 in each row. Chelae 84μ long, both digits dentate; pilus dentilis slender, arthrodial filaments at base of movable digit subequal in length.

Dorsal shield relatively broad, with an overall reticular pattern, well sculptured, especially anteriorly. $DL=1235-1264\mu$; $DW=950-1045\mu$; $DL/DW=1.2-1.3$. The shield bears only 37 pairs of setae, px_2 and px_3 being absent. Seta r_1 distinctly longer than seta s_1 ; lengths of setae i_4 and z_2 about $1\frac{1}{2}$ times the distance between their bases; seta Z_5 about $1\frac{1}{4}$ times as long as seta J_5 .

Sternal shield with a distinct reticular pattern as well as a fine granulation, anterior and posterior margins very slightly concave. $SL=114-124\mu$; $SW=257\mu$; $SL/SW=0.4-0.5$. First pair of sternal setae relatively short, not reaching posterior margin of sternal shield; second and third pairs and metasternal setae considerably longer.

Genital shield flask-shaped, with a reticular and granular pattern. $GW_1=257-284\mu$; $GW_2=219\mu$; $GW_1/GW_2=1.2-1.3$. Genital setae relatively long, approximately equal to GW_2 , and extending to bases of second pair of flanking setae.

Anal shield with linear and granular markings, anterior margin straight or convex, anus situated at less than its length from the anterior margin. $AL=180\mu$; $AW=200-205\mu$; $AL/AW=0.9$. Paranal setae level with posterior half of anus, about $4/5$ as long as postanal seta.

Integument of idiosoma with about 37 pairs of long ventral and marginal setae, many of which are barbed. Metapodal plates broadly oval, length to width about 4 : 3.

Chaetotaxy of legs normal, anterior and posterior setae on coxa I subequal in length. Inner ventral seta on tibia II slightly shorter and stouter than outer seta; inner ventral seta on genu II slightly shorter and stouter than outer seta, but longer than in *A. marshalli*. Tarsus II bears three stout, blunt, terminal setae. Length of tarsus IV about 7 times its width at the base.

MALE (figs. 14–15): Deutosternum as in female; chelicera as illustrated. Chaetotaxy of dorsal shield as in female. $DL=1064-1092\mu$; $DW=779-884\mu$; $DL/DW=1.2-1.4$. Holoventral shield reticulate, expanded behind coxae IV, bearing 28–29 setae, 15–16 being situated in the preanal region. Chaetotaxy of legs as in female, but inner ventral seta on tibia II stouter, resembling the condition in *A. marshalli* females.

HOSTS AND LOCALITIES. *Arvicanthus niloticus* (Desmarest), Bunyoro, Uganda (types in B.M.N.H.).

Tatera valida (Bocage), Bunyoro, Uganda (S.A.I.M.R.).

Tatera species, Kerio Valley, Kenya and W. Nile district, Uganda (S.A.I.M.R.).

Rattus natalensis (Smith), an Elephant Shrew (single record) and an unidentified rodent, Kerio Valley, Kenya (S.A.I.M.R.).

Unidentified rodent, Yei, Sudan (paratype of *A. equatoriensis* Keegan in B.M.N.H.).

Androlaelaps callosus (Berlese)

Hypoaspis (*Haemolaelaps*) *callosus* Berlese, 1916, *Redia* 12 : 171.

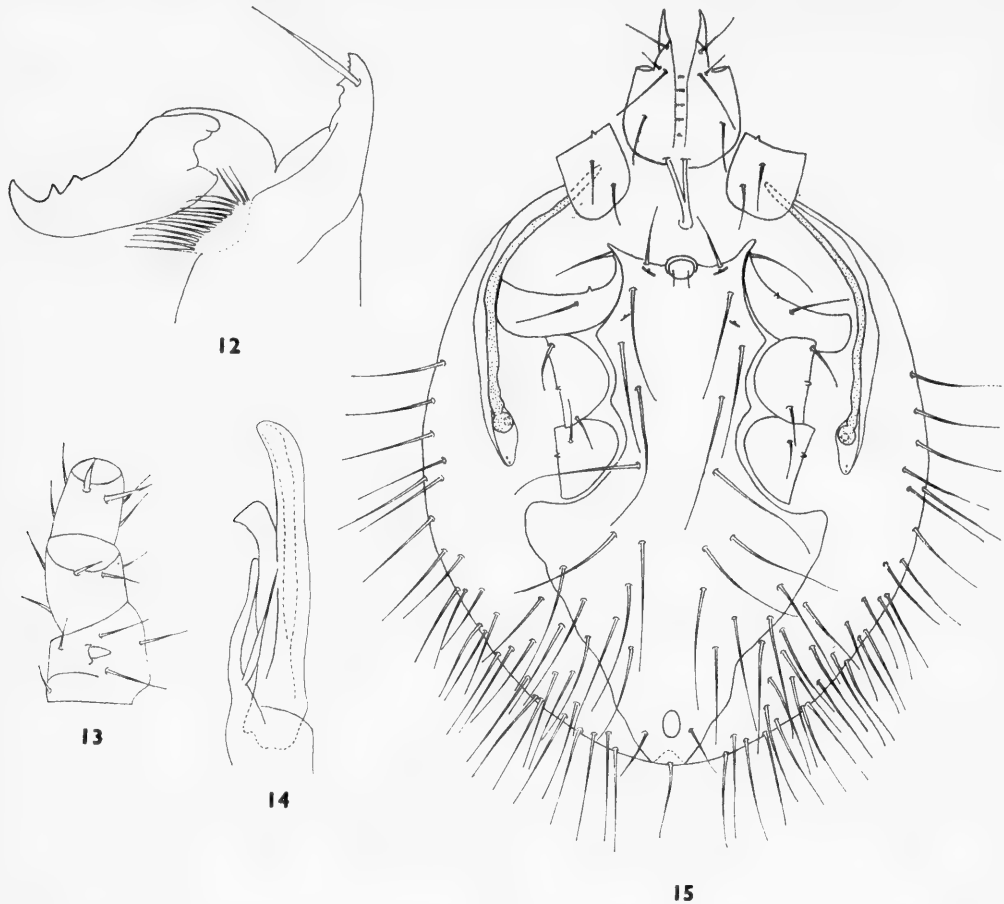
Cyclolaelaps lophuromius Radford, 1939, *Parasitology* 31 : 243, fig. 1 (*syn. nov.*).

Hypoaspis (Haemolaelaps) lophuromius, Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* 14 : 70.

Haemolaelaps lophuromius, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa*, 10 : 238.

Haemolaelaps sudanicus Zumpt & Till, 1954, *Rev. Ecuat. Ent. Parasit.* 2 : 213, fig. 3; Keegan, 1956, *J. Egypt. publ. Hlth. Ass.* 31 : 237, fig. 22 (*syn. nov.*).

FEMALE (figs. 16–19): Deutosternum with 6 rows of 2 to 4 fine teeth. Chelae 40–46 μ long; pilus dentilis with basal 4/5 inflated, apex sharply recurved according



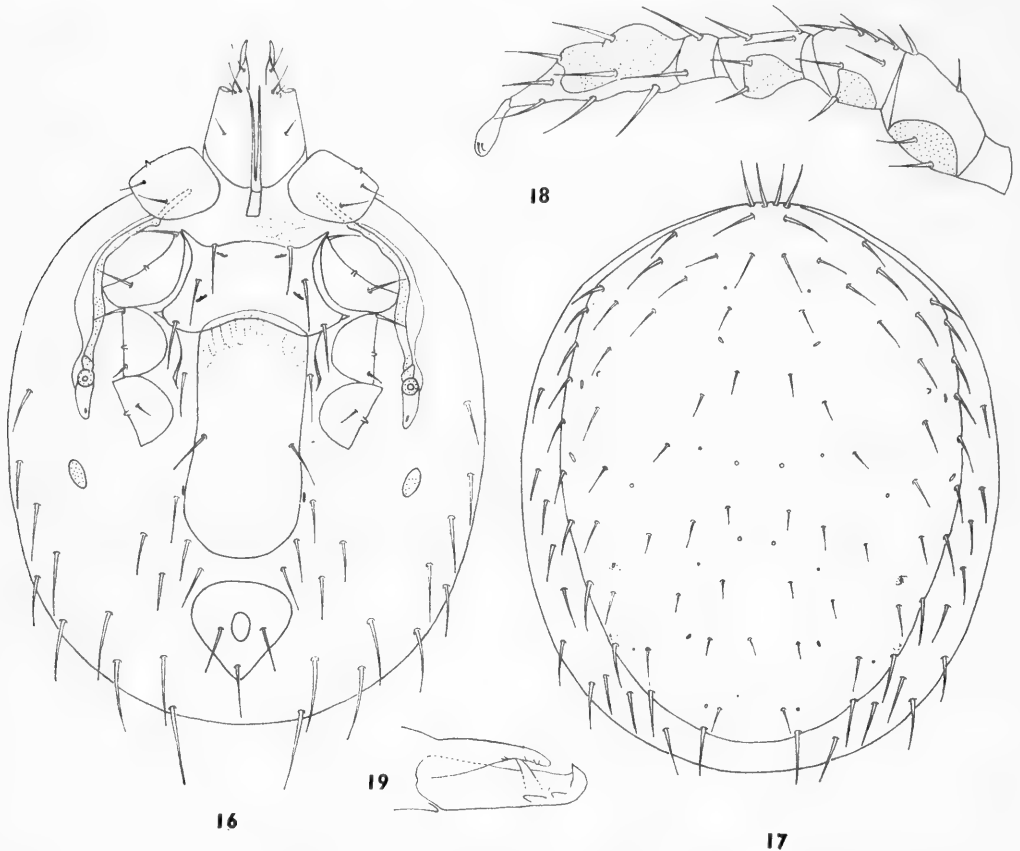
FIGS. 12–15. *Androlaelaps arvicantis* Radford. Chelicera (Fig. 12) and ventral view of femur, genu and tibia of leg II (Fig. 13) of female. Chelicera (Fig. 14) and venter (Fig. 15) of male.

to Keegan (1956) but indistinct in the specimens examined; one of the arthrodistal filaments at the base of the movable digit longer than the others.

Dorsal shield reticulate, relatively broad. DL=600–620 μ ; DW=445–486 μ ; DL/DW=1.3–1.4. It bears 39 pairs of setae and one accessory seta at the level of J4. Anterior and marginal setae longer and stouter than those on central part of shield and provided with fine barbs. Lengths of setae *i*4 and *z*2 approximately half the distance between their bases; seta *Z*5 about 1½ times as long as seta *J*5.

Sternal shield with a reticular pattern which is most pronounced antero-laterally and indistinct on the central part of the shield. $SL=83-93\mu$; $SW=134-145\mu$; $SL/SW=0.6-0.7$. Sternal setae stout, first pair the same length as the metasternal setae, second and third pairs slightly longer.

Genital shield granular and also with a reticulate pattern which is well marked



FIGS. 16-19. *Androlaelaps callosus* (Berlese), female. Venter (Fig. 16); dorsum (Fig. 17); femur, genu, tibia and tarsus of leg IV (Fig. 18); chelicera (Fig. 19).

posteriorly but less distinct anteriorly. $GW_1=130\mu$; $GW_2=118-127\mu$. Length of genital setae less than half GW_2 .

Anal shield approximately as wide as long, the length and width varying between 103μ and 114μ . Anus situated at approximately its length from the anterior margin of the shield; paranal setae level with middle of anus, slightly shorter than postanal seta.

Integument of idiosoma bears 25 pairs of ventral and marginal setae, the latter being barbed. Metapodal plates ovoid, their length to width about 2 : 1.

Chaetotaxy of legs normal; anterior seta on coxa I about $4/5$ as long as posterior seta. Length of tarsus IV $4\frac{1}{2}$ times its width at the base. This species is charac-

terized by the strongly chitinated swellings on several of the leg segments, namely, femur, tibia and tarsus of leg I, femur II, tarsus III, tibia and tarsus of leg IV.

MALE: Not known.

HOSTS AND LOCALITIES: *Lophuromys flavopunctatus* Thomas (= *Lophuromys zena*) from Kenya (Berlese, 1916; Keegan, 1956), from Kampala, Uganda (syntype of *C. lophuromius* in B.M.N.H.), and from Torit, Sudan (type series of *H. sudanicus* in S.A.I.M.R.).

Unidentified rodent from Uganda (B.M.N.H.).

Keegan (1956) records this species from *Tachyoryctes* sp. and a mixed collection of *Otomys* and *Arvicanthis* species in the Rift Valley Province, Kenya.

Androlaelaps capensis (Hirst)

Haemolaelaps capensis Hirst, 1916, *J. zool. Res.* 1 : 79, figs. 12-14.

Hypoaspis (Haemolaelaps) capensis, Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* 14 : 72.

Haemolaelaps capensis, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa*, 10 : 246.

Haemolaelaps spinatarsus Berlese, 1918, *Redia* 13 : 123; Keegan, 1956, *Trans. Amer. micr. Soc.* 75 : 314, figs. 11-12; Zumpt & Till, 1958, *J. ent. Soc. S. Afr.* 21 : 267.

Haemolaelaps mystromys Radford 1942a, *Parasitology* 34 : 300, figs. 3-4 (*syn. nov.*).

FEMALE (figs. 20-22): Deutosternum with 6 rows of 3-4 small teeth. Chelae 56-64 μ long; pilus dentilis slender; arthrodial filaments subequal in length.

Dorsal shield ovoid, reticulate. DL=656-827 μ ; DW=394-500 μ ; DL/DW=1.6-1.7. It bears 39 pairs of setae of moderate length, one or two unpaired accessory setae sometimes being present. Lengths of *i*₄ and *z*₂ about 4/5 the distance between their bases; anterior and marginal setae a little longer; seta *Z*₅ at least 1½ times as long as *J*₅.

Sternal shield reticulate, merging anteriorly with presternal area, pattern weakly developed posteriorly. SL=105-133 μ ; SW=142-150 μ ; SL/SW=0.7-0.9.

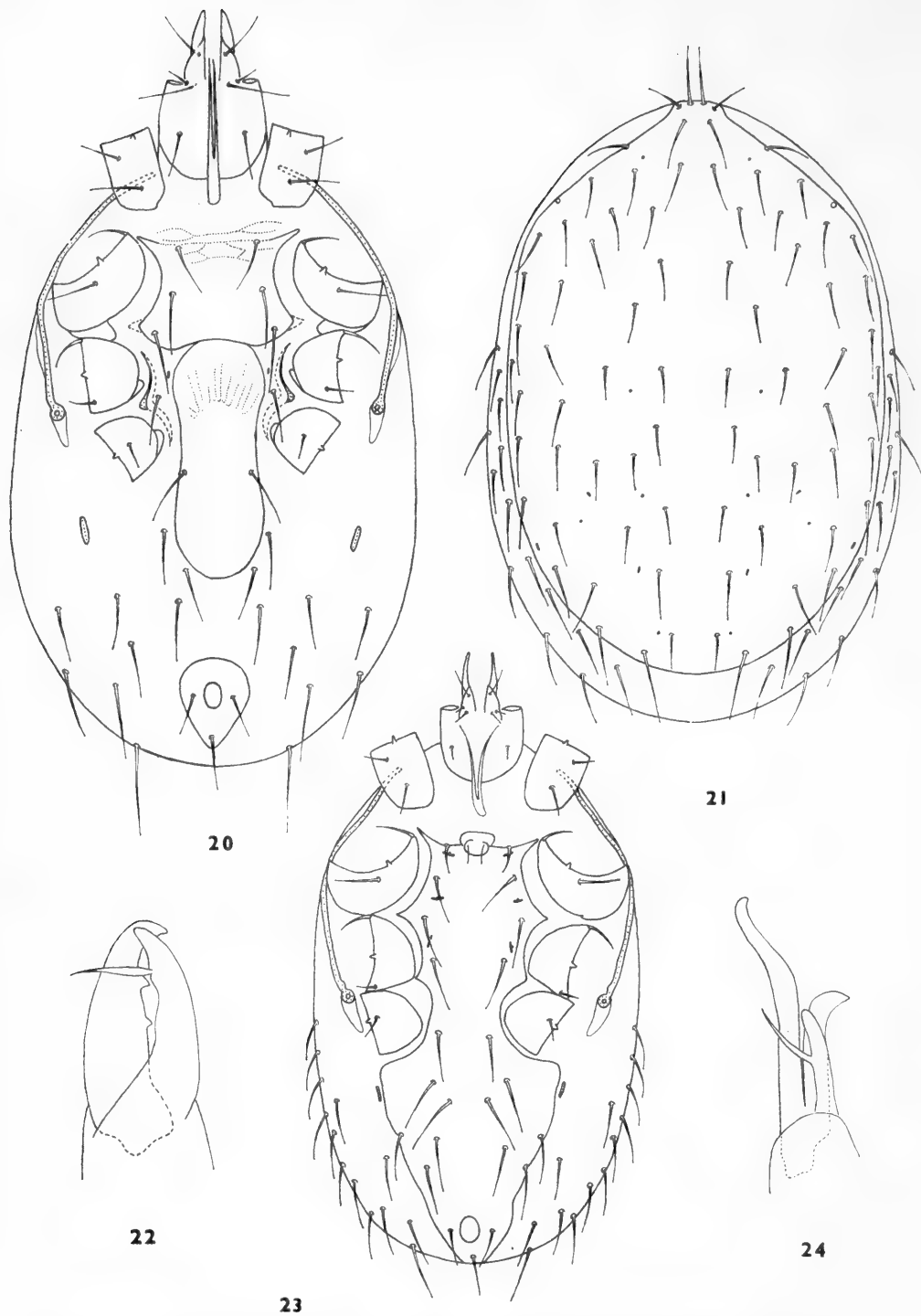
Genital shield apparently smooth, rather slender, and may be slightly widened behind the genital setae. GW₁=102-128 μ ; GW₂=94-106 μ ; GW₁/GW₂=1.1-1.3. Length of genital setae about 2/3 GW₂.

Anal shield pear-shaped, 1.3-1.5 times longer than broad. AL=114-134 μ ; AW=76-100 μ . Anus situated at approximately its length from the anterior margin. Paranal setae level with middle of anus, about 4/5 as long as postanal seta.

Integument of idiosoma bears 23 pairs of ventral and marginal setae, some of the latter having fine barbs. Metapodal plates elongate, length to width about 4 : 1.

Chaetotaxy of legs normal. Anterior seta on coxa I about 4/5 as long as posterior seta. Tarsus II has 3 stout, blunt, terminal spines and 3 stout ventral spines. Caruncle of tarsus IV relatively long, its length being 2½ times the greatest width of the tarsus. Length of tarsus IV about 8 times its width at the base.

MALE (figs. 23-24): Chelicera as figured, with a slender pilus dentilis. Dorsal shield reticulate, chaetotaxy as in female. DL=570 μ ; DW=323 μ ; DL/DW=1.8. Holoventral shield reticulate, with 23 setae. Integument bears about 23 pairs of marginal and ventral setae. Chaetotaxy of legs as in female, but femur II with a stout spur.



FIGS. 20-24. *Androlaelaps capensis* (Hirst). Venter (Fig. 20), dorsum (Fig. 21) and chelicera (Fig. 22) of female, Venter (Fig. 23) and chelicera (Fig. 24) of male.

HOSTS AND LOCALITIES. *Cryptomys hottentotus* (Lesson), Grahamstown, Cape Province (type series in B.M.N.H.) and several localities in Natal and the Transvaal (S.A.I.M.R.).

Cryptomys holosericeus (Wagner), Kruger National Park, Transvaal (S.A.I.M.R.).

Georychus capensis (Pallas), Knysna, Cape Province (S.A.I.M.R.).

Myxomys albicaudatus (Smith), Albany, Cape Province (types of *H. myxomys* in B.M.N.H.).

Androlaelaps casalis (Berlese)

Iphis casalis Berlese, 1887, *Acari, Myr. Scorp. Ital. Fasc.* 38 N.8, figs. 3-5.

Haemolaelaps casalis, Bregetova, 1956, *Acad. Sci. U.S.S.R.* 61 : 89 & 99, figs. 143-4.

Hypoaspis oculatus Oudemans, 1915, *Arch. Naturgesch.* (A) 81 : 134.

Haemolaelaps molestus Oudemans, 1929, *Ent. Ber.* 8 (169) : 13; Willmann, 1939, *Abh. Nat. Ver. Bremen* 31 : 173, figs. 5-7.

Atricholaelaps megaventralis Strandtmann, 1947, *Proc. ent. Soc. Wash.* 49 : 112.

Hypoaspis freemani Hughes, 1948, Mites associated with stored food products: 129, figs. 173-179; Strandtmann, 1956, *J. Kansas ent. Soc.* 29 : 138.

Haemolaelaps haemorrhagicus Asanuma, 1952, *Misc. Rep. Res. Inst. Nat. Res.* No. 25 : 87, fig. 1.

(For further references see Strandtmann & Wharton, 1958, *Manual of Mesostigmatid Mites*: 34).

FEMALE (figs. 25-27): Deutosternum with 6 rows each of 5 fine teeth. Chelae 34-40 μ long; pilus dentilis slender; arthrodial filaments subequal in length.

Dorsal shield oval, reticulate. DL=620-710 μ ; DW=376-429 μ ; DL/DW=1.5-1.7. It bears 39 pairs of symmetrically arranged setae, as well as a variable number of unpaired accessory setae between the *J* series. Setae *i*₄ and *z*₂ are longer than half the distance between their bases; the longer posterior setae are barbed; seta *Z*₅ is 1 $\frac{1}{4}$ -1 $\frac{1}{2}$ times as long as *J*₅.

Sternal shield reticulate; SL=86-96 μ ; SW=124-140 μ ; SL/SW=0.7-0.8. First pair of sternal setae about as long as the metasternal setae, but a little coarser; second and third pairs of sternal setae slightly longer than first pair.

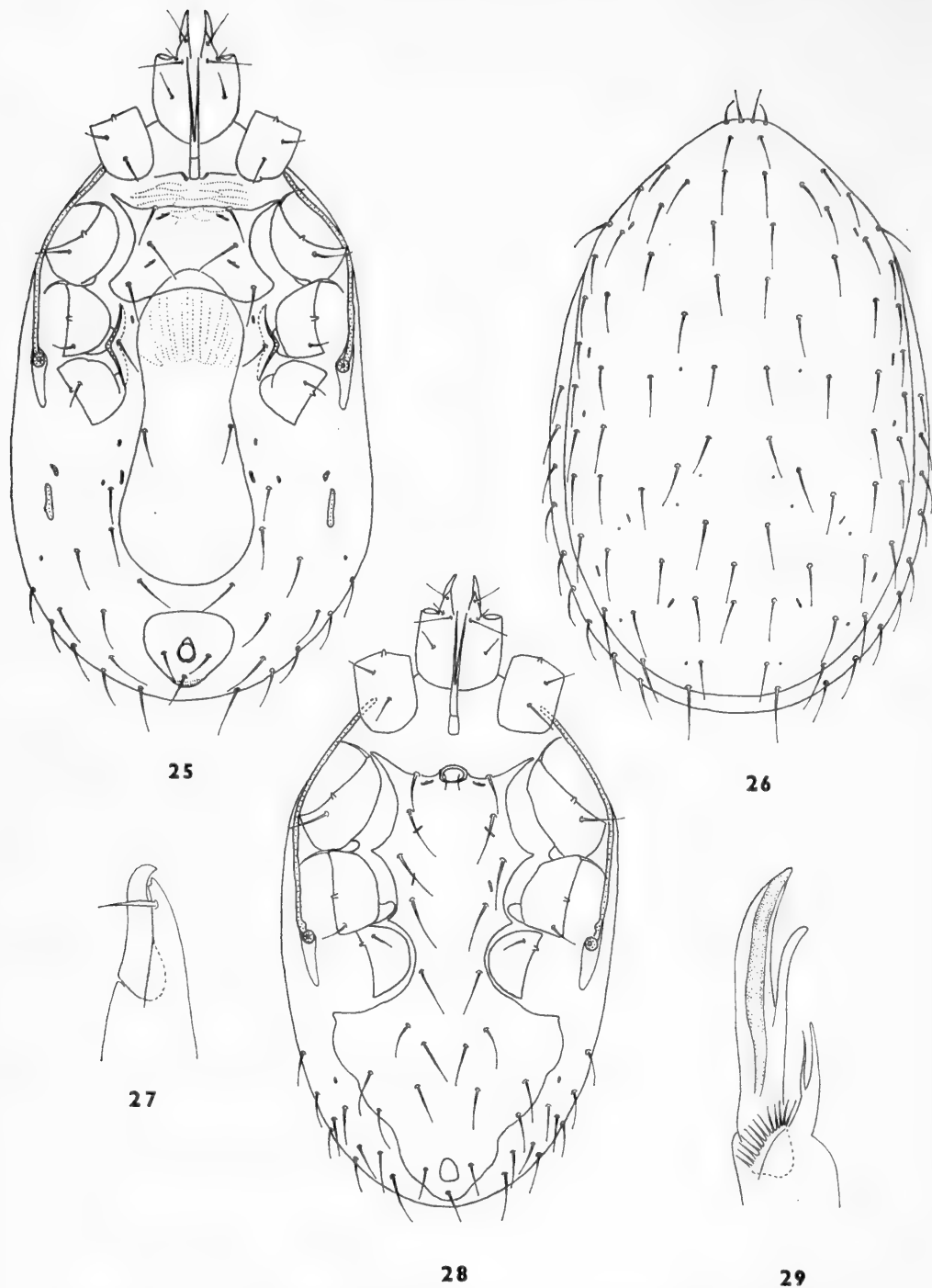
Genital shield expanded and broadly rounded posteriorly, with a well-defined reticulate pattern which extends at least as far as the anterior flap of the shield. GW₁=143-166 μ ; GW₂=96-105 μ ; GW₁/GW₂=1.4-1.6. Genital setae short, less than half GW₂.

Anal shield reticulate, approximately as long as broad. AL=90-114 μ ; AW=96-114 μ . Anus situated at about its length from the anterior margin. Paranal setae inserted on a level between middle and posterior end of anus, and approximately the same length as the postanal seta.

Integument of idiosoma bears about 21 pairs of ventral and marginal setae. Metapodal plates elongate, length 4-7 times the width.

Chaetotaxy of legs normal. Posterior seta on coxa I slightly longer than anterior seta. Three ventral and 3 apical setae on tarsus II are thickened, but do not form blunt spines. Setae generally rather fine and of moderate length. Length of tarsus IV about 6 times width at base.

MALE (figs. 28-29): Chelicerae as figured, the fixed digit bearing a slender pilus dentilis. Chaetotaxy of dorsal shield as in the female. DL=466-485 μ ; DW=



FIGS. 25-29. *Androlaelaps casalis* (Berlese). Venter (Fig. 25), dorsum (Fig. 26) and chelicera (Fig. 27) of female. Venter (Fig. 28) and chelicera (Fig. 29) of male.

284–322 μ ; DL/DW=1.5–1.6. Holoventral shield reticulate, expanded behind coxae IV, bearing 23 setae. Chaetotaxy of legs as in female.

HOSTS AND LOCALITIES: Cosmopolitan, from a wide variety of bird and mammalian hosts, and also found in straw, hay, detritus, etc. Recorded from the Ethiopian region from *Rattus rattus* (Linnaeus) and *Xerus inauris* (Zimmermann), Transvaal, and from *Sciurus carolinensis* Gmelin, Cape Province (S.A.I.M.R.).

Androlaelaps centrocarpus (Berlese)

Haemolaelaps centrocarpus Berlese, 1911, *Redia* 7: 432; Costa, 1961, *Bull. Brit. Mus. (nat. Hist.) Zool.* 8: 27, figs. 39–44.

Haemolaelaps mauritanicus Hirst, 1925, *Bull. Com. Etud. Hist. Sci.*: 98, fig. 3 (*syn. nov.*).

FEMALE (figs. 30–32): Deutosternum with 6 rows of 2–3 teeth. Chelae 60 μ long; pilus dentilis slightly inflated, tapering towards the tip; arthrodial filaments subequal in length.

Dorsal shield reticulate, widest at level of setae *r*6, then tapering gradually posteriorly. DL=836–911 μ ; DW=485–523 μ ; DL/DW=1.7–1.8. The shield bears additional paired setae in the *ax* and *px*1 positions, as well as numerous unpaired setae on the postero-median part and extending anteriorly as far as setae *i*5. The setae are long and subequal in length, except for *J*5, which are shorter. Lengths of setae *i*4 and *z*2 approximately 1½ times the distance between their bases; seta *Z*5 at least 1½ times as long as seta *J*5. Some marginal setae have fine barbs.

Sternal shield reticulate. SL=105–130 μ ; SW=180–190 μ ; SL/SW=0.6–0.7. Metasternal setae relatively short, approximately half as long as the sternal setae.

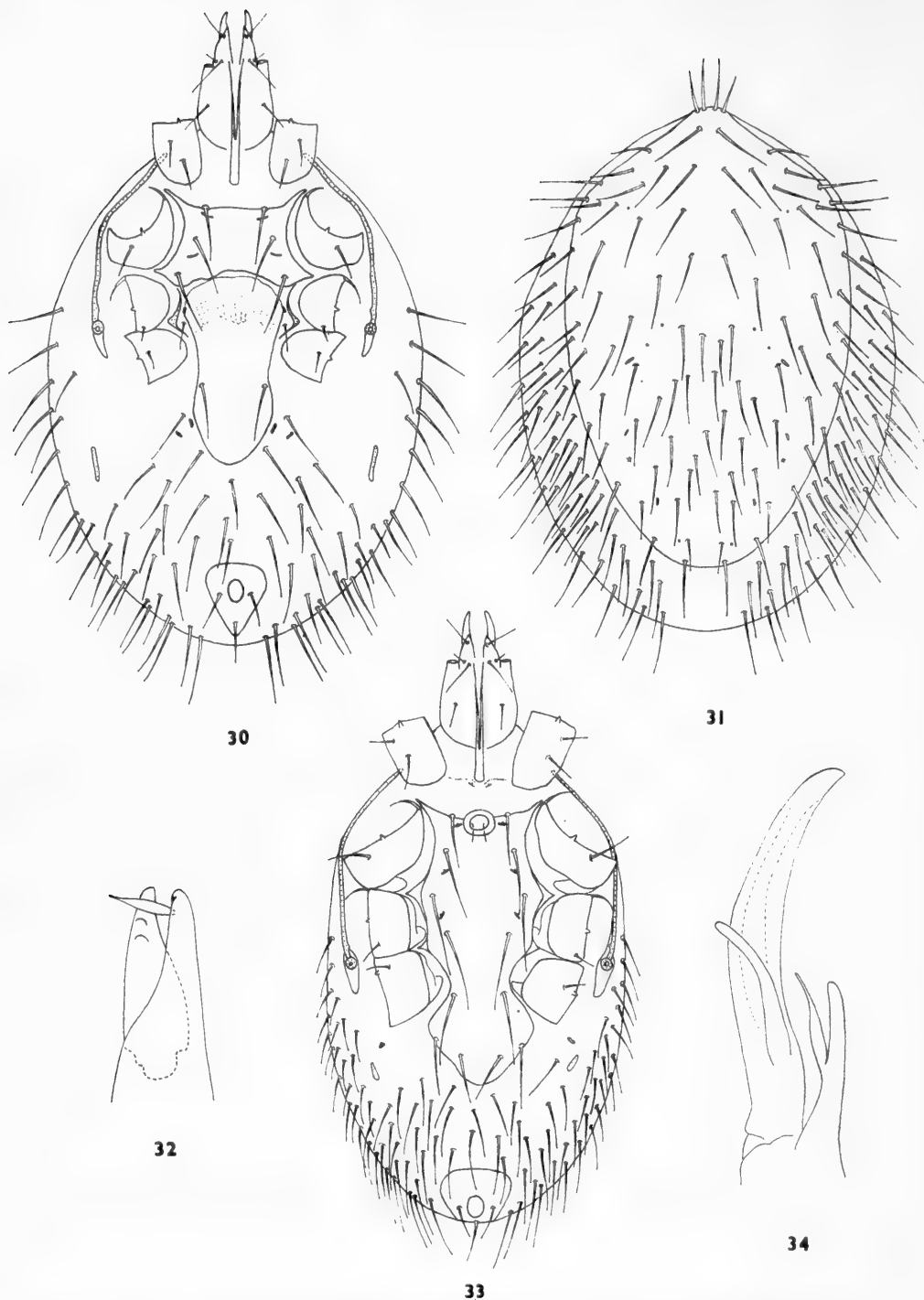
Genital shield granular, with a weakly defined reticular pattern posteriorly; slightly widened behind the genital setae, then tapering abruptly. GW₁=143–162 μ ; GW₂=130–143 μ ; GW₁/GW₂=1.1. Genital setae fairly long, about 4/5 GW₂, reaching to base of second pair of flanking setae.

Anal shield pear-shaped, anterior margin straight. AL=120–145 μ ; AW=110–124 μ ; AL/AW=1.1–1.3. Anus situated at less than its length from the anterior margin. Paranal setae level approximately with middle of anus, very slightly longer than postanal seta.

Integument of idiosoma bears numerous long ventral and marginal setae, many of the latter being barbed. Metapodal plates elongate, length to width about 6:1.

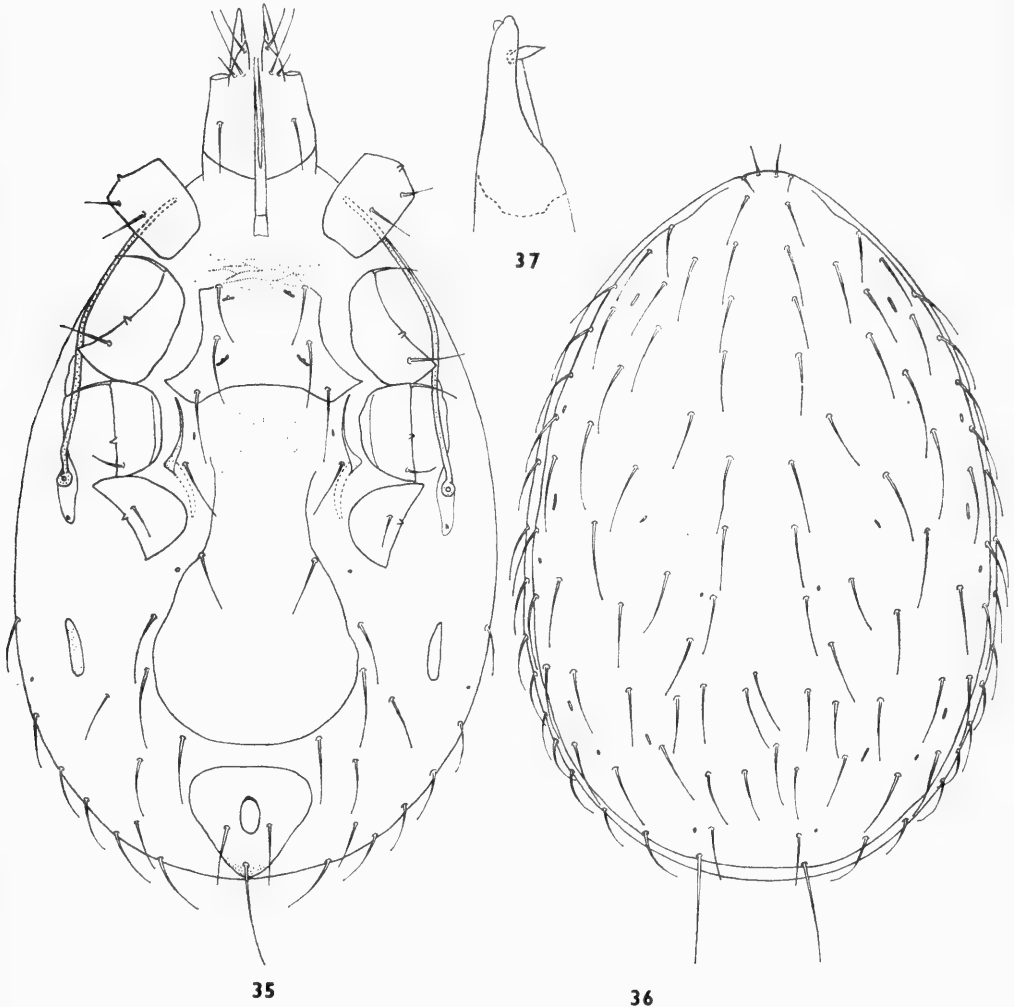
Chaetotaxy of legs normal except that tibia III bears 9 setae. Posterior seta of coxa I thicker than anterior seta, but approximately the same length. Femur I has 2 short, stout, spine-like setae on its dorsal surface, and trochanter I has a stout, spine-like dorsal seta. Leg II has a ventral spine-like seta on the trochanter, femur and genu, and 2 on the tibia. Tarsus II has 3 spine-like ventral setae, and 3 stout, blunt, apical setae. The upper dorsal seta on trochanter IV is considerably thicker than the other setae on this segment. Length of tarsus IV nearly 10 times width at base.

MALE (figs. 33–34): Chelicerae as figured, with a pilus dentilis resembling that of the female. Dorsal shield as in female. And shield separated from sternito-ventral shield, the latter strongly reticulate and bearing 7 pairs of setae, 2 pairs being placed on the area posterior to coxae IV. Chaetotaxy of legs as in female.



FIGS. 30-34. *Androlaelaps centrocarpus* (Berlese). Venter (Fig. 30), dorsum (Fig. 31) and chelicera (Fig. 32) of female. Venter (Fig. 33) and chelicera (Fig. 34) of male.

HOSTS AND LOCALITIES. Berlese recorded this species from "Mures" in British Somaliland. The above description is based on females from *Taterillus* species, Kerio Valley, Kenya (S.A.I.M.R.) and on males from *Gerbillus gerbillus* Olivier, Israel (received by courtesy of Dr. M. Costa).

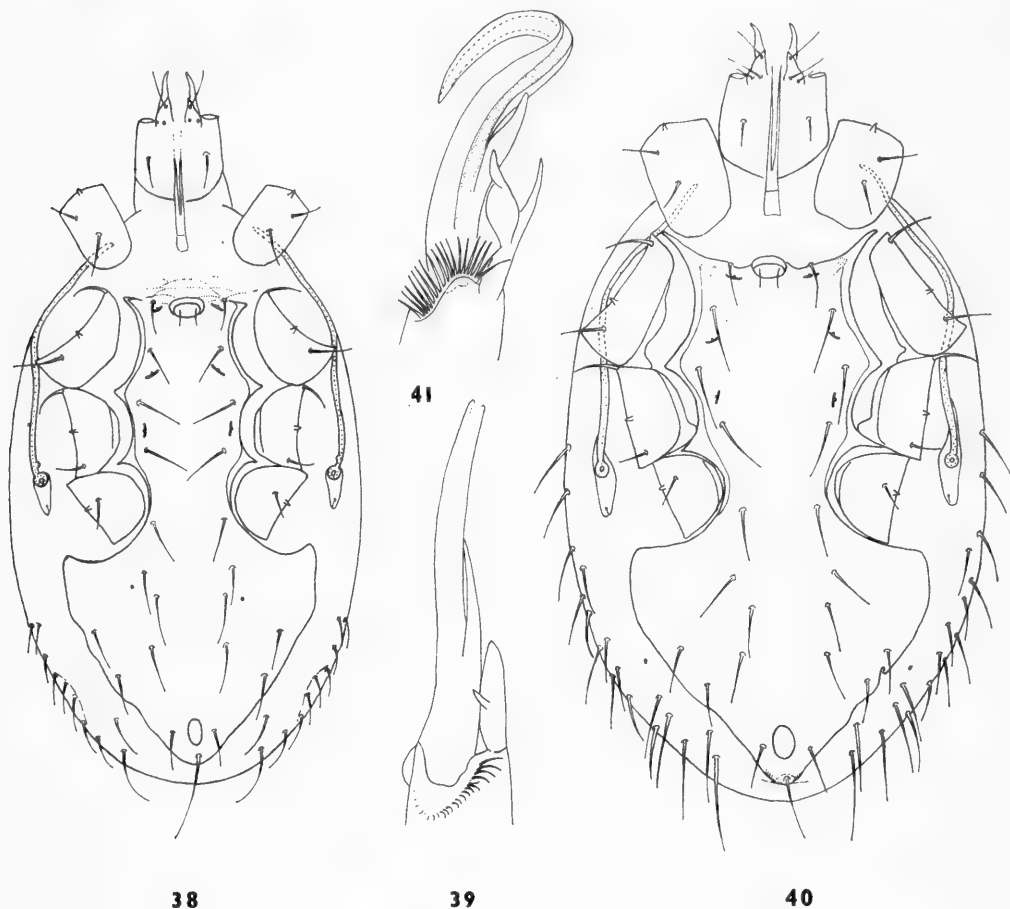


FIGS. 35-37. *Androlaelaps congoensis* sp. nov., female. Venter (Fig. 35); dorsum (Fig. 36); chelicera (Fig. 37).

NOTE: The specimens described above have been compared with drawings of the type made by Dr. G. O. Evans. *Haemolaelaps mauritanicus* Hirst, from *Gerbillus pyramidum* Geoffroy, Mauritania, is most probably a synonym of *A. centrocarpus*. It is slightly smaller, its setae are relatively finer, and the ventral setation is more symmetrical than in *A. centrocarpus*.

Androlaelaps congoensis sp. nov.

FEMALE (figs. 35-37): Deutosternum with 6 rows of 3-5 very fine teeth and an ill-defined 7th row with 4 minute teeth. Chelae 48μ long, pilus dentilis small, slightly inflated, terminating in a sharp point; arthrodial filaments short, subequal in length.



FIGS. 38-41. *Androlaelaps congoensis* sp. nov., venter (Fig. 38) and chelicera (Fig. 39) of male.

Androlaelaps cricetomydis sp. nov., venter (Fig. 40) and chelicera (Fig. 41) of male.

Dorsal shield reticulate. $DL=703-722\mu$; $DW=456-504\mu$; $DL/DW=1.4-1.6$. The shield bears the usual 39 pairs of setae as well as 11-13 unpaired accessory setae between the *J* series. Lengths of setae *i*₄ and *z*₂ approximately equal to the distance between their bases; seta *Z*₅ twice as long as seta *J*₅. Setae all apparently simple except seta *Z*₅ which has very fine barbs.

Sternal shield reticulate, merging with presternal area. SL (from level of first

sternal setae)=105 μ ; SW=114-120 μ ; SL/SW=0.9. Sternal and metasternal setae subequal in length.

Genital shield patterned posteriorly, greatly expanded. $GW_1=205-219\mu$; $GW_2=114-133\mu$; $GW_1/GW_2=1.6-1.8$. Genital setae relatively short, slightly more than half GW_2 .

Anal shield broader than long. AL=109 μ ; AW=124 μ ; AL/AW=0.9. Anus situated at approximately its length from the anterior margin of the shield. Paranal setae near posterior margin of anus, extending beyond base of postanal seta and about 3/5 as long as postanal seta.

Integument of idiosoma bears 21 pairs of ventral and marginal setae, all apparently simple. Metapodal plates elongate, length about 4 times the breadth.

Genu III bears 10 setae and tibia III has 9. Anterior seta on coxa I is about 2/3 as long as posterior seta. Posterior ventral seta on femur IV extremely long, about 3/5 the total length of the femur. Tarsus IV long and slender, its length about 7 times its width at the base.

MALE (figs. 38-39): Deutosternum with 4 rows of very fine teeth, the 5th and 6th rows ill defined. Fixed digit of chelicera bears a short pilus dentilis, as in the female; spermadactyl about 80 μ long.

Dorsal shield 560 μ long, 330 μ wide. Holoventral shield bears 23 setae. Chaetotaxy of legs as in female.

HOSTS AND LOCALITIES: Holotype (♀), allotype (♂) and 7 female paratypes (1933.II.14.309-318 part) collected by F. W. J. Cox from the nest of *Spermestes cucullatus* Swainson at Mulungu, Belgian Congo, 5 November, 1919. This species appears to be very common in birds' nests and has also been found in the nests of a serin finch, weaver, oriole, sparrow, bunting and wagtail, all from Zomba, Nyasaland. The specimens are all in the collection of the British Museum (Natural History).

Androlaelaps cricetomydis sp. nov.

FEMALE (figs. 42-44): Deutosternum bears 6 rows of 3-4 small teeth. Chelae about 45 μ long; pilus dentilis inflated; arthrodial filaments subequal in length.

Dorsal shield reticulate, widest between the posterior setae S_1 and S_2 . DL=850-883 μ ; DW=560-599 μ ; DL/DW=1.5. The shield bears 39 pairs of setae, accessory setae being absent; setae on central part of shield relatively short, lengths of s_4 and z_2 being less than half the distance between their bases. Marginal setae longer, coarser and barbed; S_1 more than twice as long as J_1 , Z_5 about 1½ times as long as J_5 .

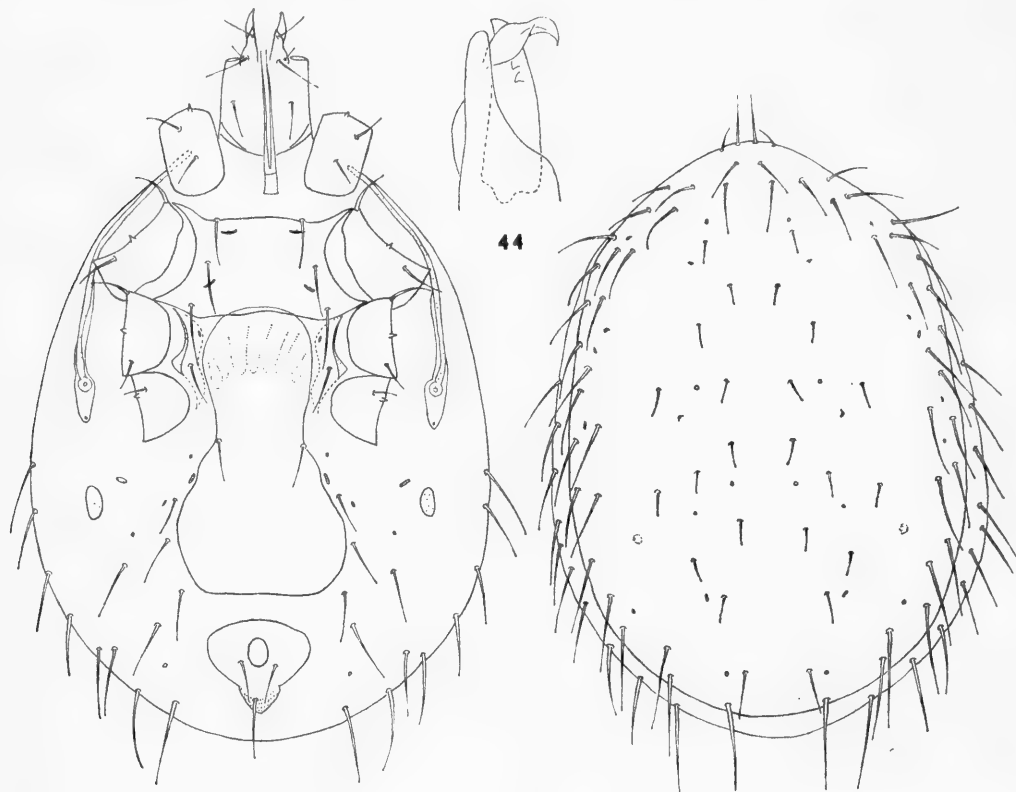
Sternal shield reticulate, heavily sclerotized. SL=128-138 μ ; SW=190-195 μ ; SL/SW=0.7.

Genital shield greatly expanded behind the genital setae, posterior margin straight or slightly concave. The reticulate pattern extends anterior to the genital setae where it becomes less well defined. $GW_1=238-247\mu$; $GW_2=128-138\mu$; $GW_1/GW_2=1.8-1.9$. Genital setae relatively short, less than half GW_2 .

Anal shield slightly broader than long. AL=133-144 μ ; AW=152 μ . Anus

situated at less than its length from the anterior margin. Paranal setae level with posterior margin of anus, about $\frac{3}{4}$ as long as postanal seta.

Integument of idiosoma bears about 23 pairs of marginal and ventral setae. The 3 pairs of ventral setae which flank the genital shield are apparently simple, the remaining ventral and marginal setae are barbed. Metapodal plates approximately twice as long as broad.

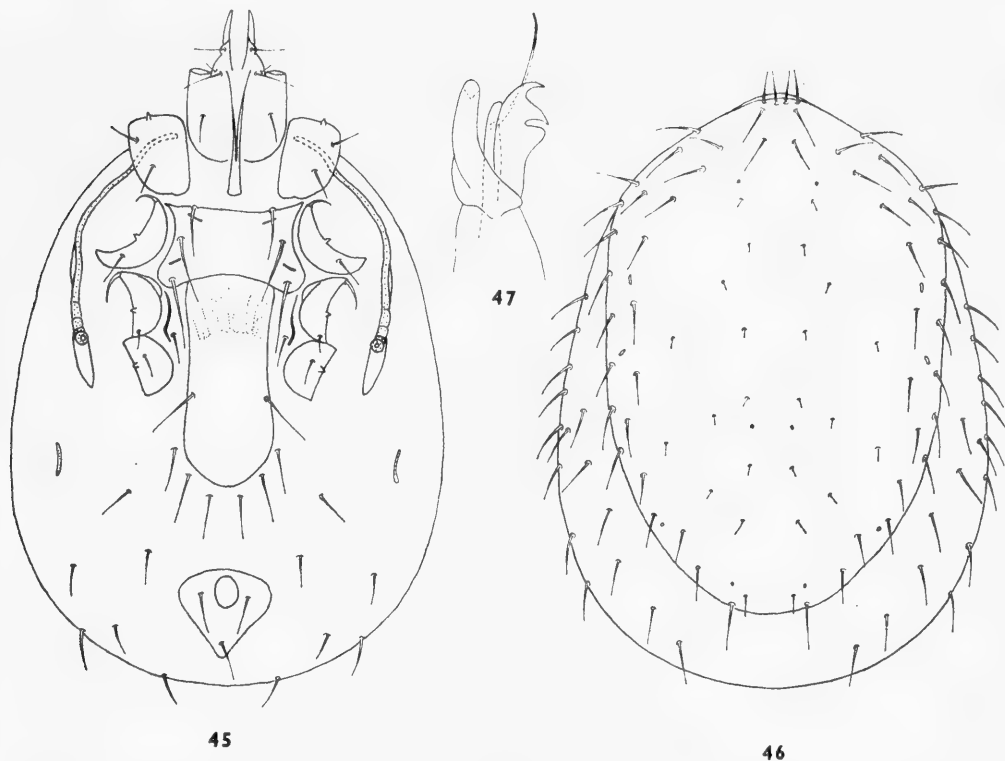


FIGS. 42-44. *Androlaelaps cricetomydis* sp. nov. Venter (Fig. 42), dorsum (Fig. 43) and chelicera (Fig. 44) of female.

Chaetotaxy of legs normal, except that tibia III bears 9 instead of 8 setae. Tarsus II bears 3 stout, ventral setae; terminal setae not particularly stout. Anterior and posterior setae on coxa I approximately equal in length. Length of tarsus IV about $6\frac{1}{2}$ times its width at the base.

MALE (figs. 40-41): Deutosternum bears 6 rows of 2-5 teeth; pilus dentilis inflated basally. Dorsal shield 650μ long, 437μ wide; chaetotaxy similar to that of female. Holoventral shield reticulate, expanded behind coxae IV and bearing 23 setae, 5 pairs lying in the region between coxae IV and the anus. Chaetotaxy of legs similar to that of the female.

HOST AND LOCALITY: The mites, received from Mr. H. J. Disney, were found in the food store of *Cricetomys gambianus* Waterhouse, Malengo Highlands, Tanganyika, 30 August, 1960. Holotype female (1962.6.12.1), allotype male (1962.6.12.2) and ten female paratypes (1962.6.12.3-7) in the collection of the British Museum (Natural History).



FIGS. 45-47. *Androlaelaps cryptomius* (Radford), female. Venter (Fig. 45); dorsum (Fig. 46); chelicera (Fig. 47).

Androlaelaps cryptomius (Radford)

Ischnolaelaps cryptomius Radford, 1939, *Parasitology* 31 : 248, fig. 5.

Hypoaspis (*Haemolaelaps*) *cryptomius*, Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* 14 : 71.

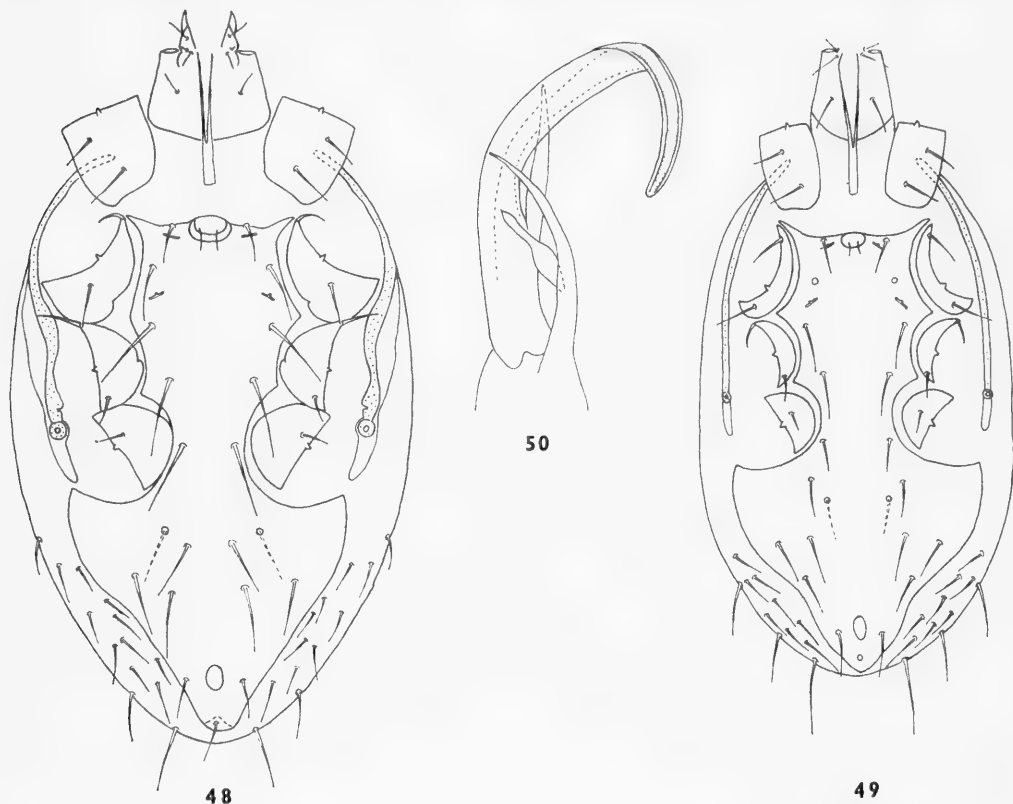
Haemolaelaps cryptomius, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 241.

Liponyssus lawrencei Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* 14 : 89, fig. 10; Zumpt & Till, 1953, *S. Afr. J. Med. Sci.* 18 : 8 (*syn. nov.*).

FEMALE (figs. 45-47): Deutosternum provided with 6 rows of teeth, 2 large and 2 small teeth in the first row, 1 large tooth in the 2nd to 5th rows, and 2 small teeth in the sixth row. Anterior rostral seta about $1\frac{1}{2}$ times as long as capitular seta. Chelae small, about 24μ long. Fixed digit weakly sclerotized, bearing a long, slender pilus dentilis; movable digit in two parts, one part edentate except for terminal hook, the other part weakly sclerotized but with large teeth. Arthrodial filaments not distinct in the specimens examined.

Dorsal shield widest at the level of setae r_5 , with a reticulate and granular pattern. $DL=508-530\mu$; $DW=350-385\mu$; $DL/DW=1.4-1.5$. The shield bears 39 pairs of setae. Those on the central part are short and fine, the lengths of setae i_4 and z_2 being less than $1/5$ the distance between their bases. The anterior and marginal setae are longer, and seta Z_5 is approximately $2\frac{1}{2}$ times as long as seta J_5 .

Sternal shield granular, with some reticulation near the lateral margins; presternal area reticulate. $SL=70-75\mu$; $SW=130-140\mu$; $SL/SW=0.5-0.6$. First pair of



FIGS. 48-50. *Androlaelaps cryptomius* (Radford), venter of male (Fig. 48). *Androlaelaps dasymys* (Radford), venter (Fig. 49) and chelicera (Fig. 50) of male.

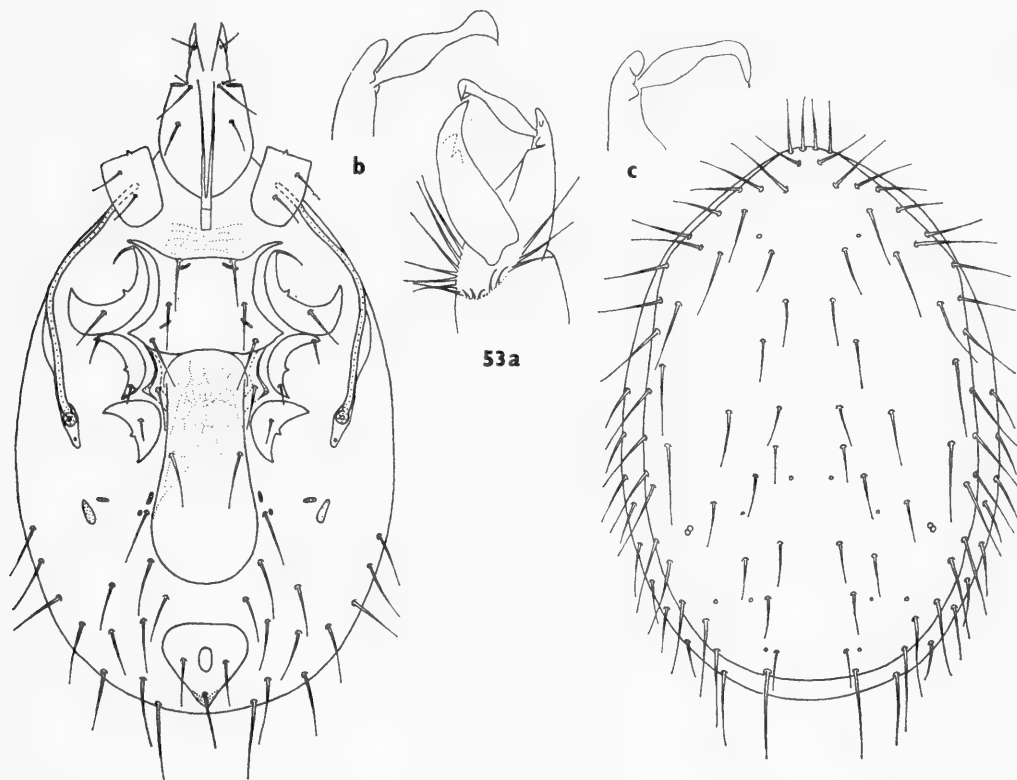
sternal setae $4/5$ as long as second and third pairs: metasternal setae about half as long as first pair of setae.

Genital shield relatively short, granular, very slightly widened behind the genital setae, with a weakly defined reticular pattern. $GW_1=96-104\mu$; $GW_2=84-88\mu$. Genital setae relatively long, about $2/3$ GW_2 .

Anal shield approximately as long as broad, length and width varying between 94μ and 104μ . Anus situated very close to anterior margin. Paranal setae level approximately with middle of anus, slightly longer than postanal seta, but not reaching the base of the latter.

Integument of idiosoma bears about 24 pairs of ventral and marginal setae. Metapodal plates elongate, their length to width about 8 : 1.

Chaetotaxy of legs normal. Posterior seta on coxa I very slightly longer and thicker than anterior seta. The leg setae are all simple and are not modified to form thickened or blunt spines. Length of tarsus IV 5–6 times its width at the base.



51

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FIGS. 51–53. *Androlaelaps dasymys* (Radford), female (from *Mystromys albicaudatus*)
Venter (Fig. 51); dorsum (Fig. 52); chelicera (Fig. 53a). Pilus dentilis of specimens
from *Tatera afra* (Fig. 53b) and *Otomys* sp. (Fig. 53c).

MALE (fig. 48): Structure of the chelicerae not very distinct in the only specimen available, but there appears to be a flagellar pilus dentilis as in the female. Dorsal shield similar to that of the female, but setae on central part relatively longer. $DL=475\mu$; $DW=284\mu$; $DL/DW=1.7$. Holoventral shield expanded behind coxae IV and bears 21 setae. The shield has an overall reticulate pattern, and also a granular appearance especially anterior to coxae IV. Chaetotaxy of legs as in female.

HOSTS AND LOCALITIES: *Georychus capensis* (Pallas) from Wynberg, Cape Province

(types in Dr. Radford's collection and M.R.A.C.), and from Knysna and Drostdy, Cape Province (S.A.I.M.R.).

***Androlaelaps dasymys* (Radford) (s. lat.)**

Ischnolaelaps dasymys Radford, 1939, *Parasitology* 31 : 245, fig. 2.

Hypoaspis (*Haemolaelaps*) *dasymys*, Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* 14 : 73.

Haemolaelaps dasymys, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 247.

Hypoaspis (*Haemolaelaps*) *labuschagnei* Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* 14 : 85, fig. 7 (syn. nov.).

Haemolaelaps davisi Zumpt & Till, 1956, *Z. Parasitenk* 17 : 287, figs. 5-8 (syn. nov.).

FEMALE (figs. 51-53): Deutosternum with 6 rows of 3-4 teeth, one tooth in each row being larger than the others in some specimens. Chelae 50-65 μ long; pilus dentilis as figured, its terminal portion appearing either swollen or ribbon-like, depending on the orientation; two or three of the arthroal filaments distinctly longer than the others.

Dorsal shield reticulate, with 39 pairs of setae; unpaired accessory setae may be present (2-6) or absent. Lengths of setae *i4* and *z2* at least 4/5 the distance between their bases, up to 1.4 times this distance in specimens from *Tatera afra*, *Rattus rattus*, *Parotomys* species, and some specimens from *Otomys* species. Marginal setae coarse, barbed; seta *Z5* 1.6-2.5 times as long as seta *J5*. $DL=822-1064\mu$; $DW=516-750\mu$; $DL/DW=1.4-1.7$.

Sternal shield reticulate, sharply demarcated from presternal area. $SL=123-163\mu$; $SW=154-200\mu$; $SL/SW=0.8-1.0$. Metasternal setae a little shorter than first pair of sternal setae, second and third pairs of sternal setae slightly longer than first pair.

Genital shield with a distinct reticulate pattern extending almost to the anterior extremity. $GW_1=170-209\mu$; $GW_2=114-165\mu$; $GW_1/GW_2=1.3-1.5$. Length of genital seta slightly more than half GW_2 .

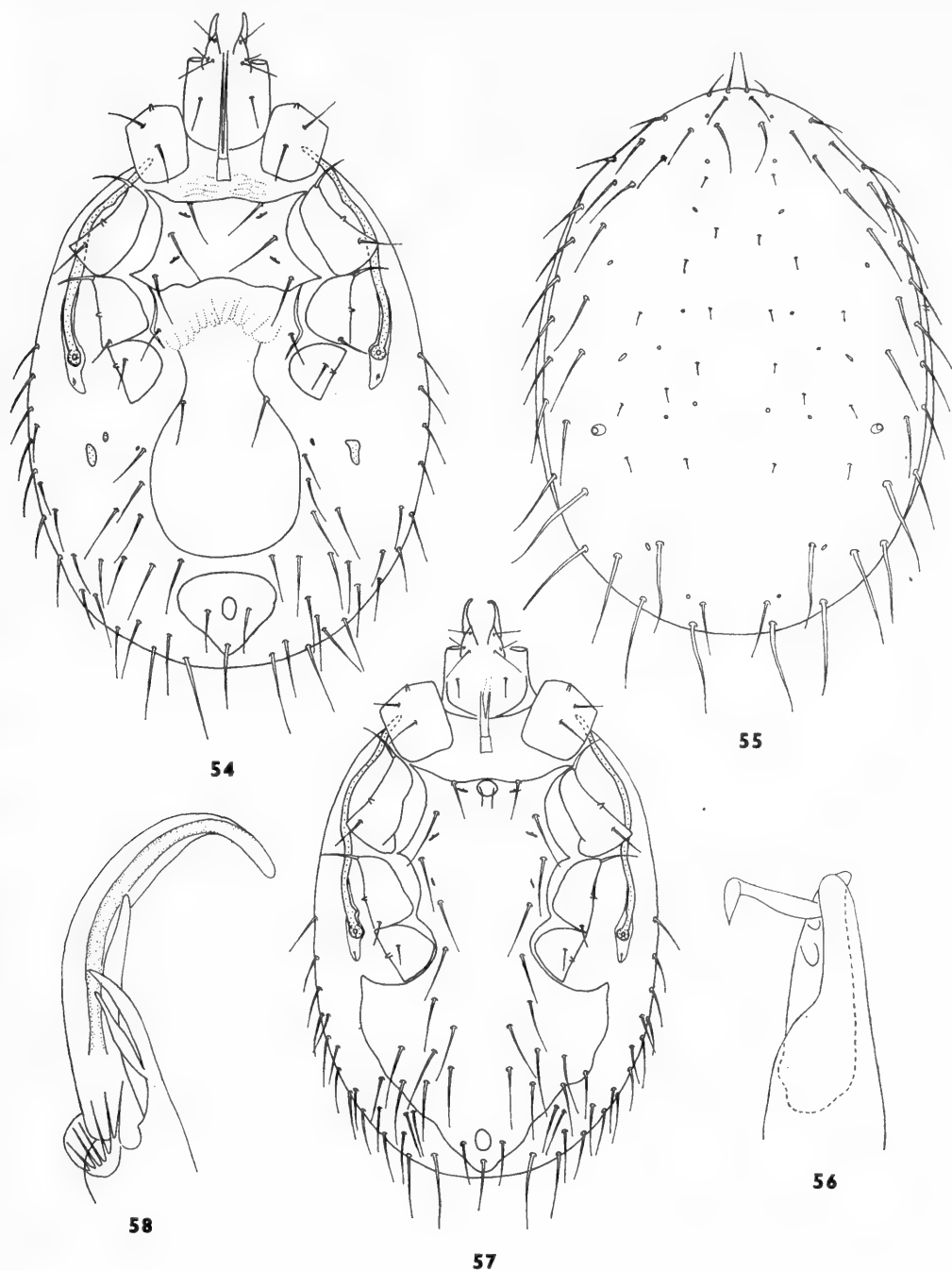
Anal shield reticulate anteriorly and laterally, approximately as long as broad. $AL=127-200\mu$; $AW=127-195\mu$. Anus situated at a little less than its length from the anterior margin; paranal setae level with middle of anus, 4/5 as long as postanal seta and extending beyond its base.

Integument of idiosoma bears 18-28 pairs of ventral and marginal setae, the latter being longer, coarser, and provided with fine barbs. Metapodal plates vary in shape from roughly elliptical to almost round, their length 1.4-2.5 times their width.

Chaetotaxy of legs normal. Posterior seta on coxa I very slightly longer and thicker than anterior seta. Tarsus II bears three stout ventral setae but no blunt spines; trochanter IV bears a stout seta on its dorsal surface. Length of tarsus IV about 7 times its width at the base.

MALE (figs. 49-50): Chelicera as figured; dorsal shield similar to that of female. $DL=684-788\mu$; $DW=418-420\mu$; $DL/DW=1.6-1.9$. Holoventral shield reticulate, expanded behind coxae IV, bearing 23 setae. Chaetotaxy of legs as in female.

HOSTS AND LOCALITIES: *Dasymys incommisus* (Sundevall), Kakumiro, Uganda (syntype of *I. dasymys* in B.M.N.H.).



FIGS. 54-58. *Androlaelaps galagus* (Lavoipierre). Venter (Fig. 54), dorsum (Fig. 55) and chelicera (Fig. 56) of female. Venter (Fig. 57) and chelicera (Fig. 58) of male.

Mystromys albicaudatus (Smith) from Basutoland (type series of *H. davisi*, the figured specimens) and from Aliwal North, Cape Province (S.A.I.M.R.).

Rattus rattus (Linnaeus) from the Transvaal (type series of *H. labuschagnei* in S.A.I.M.R.).

Rattus natalensis (Smith) from Natal, Cape Province, Transvaal, Orange Free State (S.A.I.M.R.).

Rattus chrysophilus (De Winton) and *Rattus namaquensis* (Smith) (Zumpt & Till, 1961; material not re-examined).

Otomys irroratus (Brants) and *Otomys* species from several localities in South Africa (S.A.I.M.R.).

Otomys saundersiae Roberts (Zumpt & Till, 1961; material not re-examined).

Otomys sloggetti (Thomas), Basutoland (S.A.I.M.R.).

Parotomys brantsi (Smith), Port Nolloth, Cape Province (S.A.I.M.R.).

Parotomys littledalei Thomas, van Rhynsdorp, Cape Province (S.A.I.M.R.).

Tatera afra (Gray), Basutoland and Transvaal (S.A.I.M.R.).

Rhabdomys pumilio (Sparrman), Ngorongoro, Tanganyika (M.R.A.C.).

Lophuromys sikapusi (Temminck), Cameroons (Taufflieb & Mouchet, 1959).

Androlaelaps galagus (Lavoipierre)

Haemolaelaps galagus Lavoipierre, 1955, *Ann. trop. Med. Parasit.* 49 : 304, figs. 5-6.

FEMALE (figs. 54-56): Deutosternum with 6 rows each of 2 small teeth. Chelae 54-56 μ long; pilus dentilis inflated, elongate, bent near tip and terminating in a fine point; arthrodial filaments subequal in length.

Dorsal shield reticulate, bearing 39 pairs of setae. Those on the central part of the shield are very short and fine; they are extremely minute and difficult to detect in the type specimen examined (by courtesy of Dr. M. M. J. Lavoipierre), but are more conspicuous in the specimens from *Cryptomys* sp., on which the drawings are based. Some of the setae are extremely long and barbed, namely, *J*₄, *Z*₃₋₅ and *S*₄₋₅; seta *J*₄ is at least 5 times as long as *J*₁. DL=910-960 μ ; DW=605-709 μ ; DL/DW=1.3-1.5.

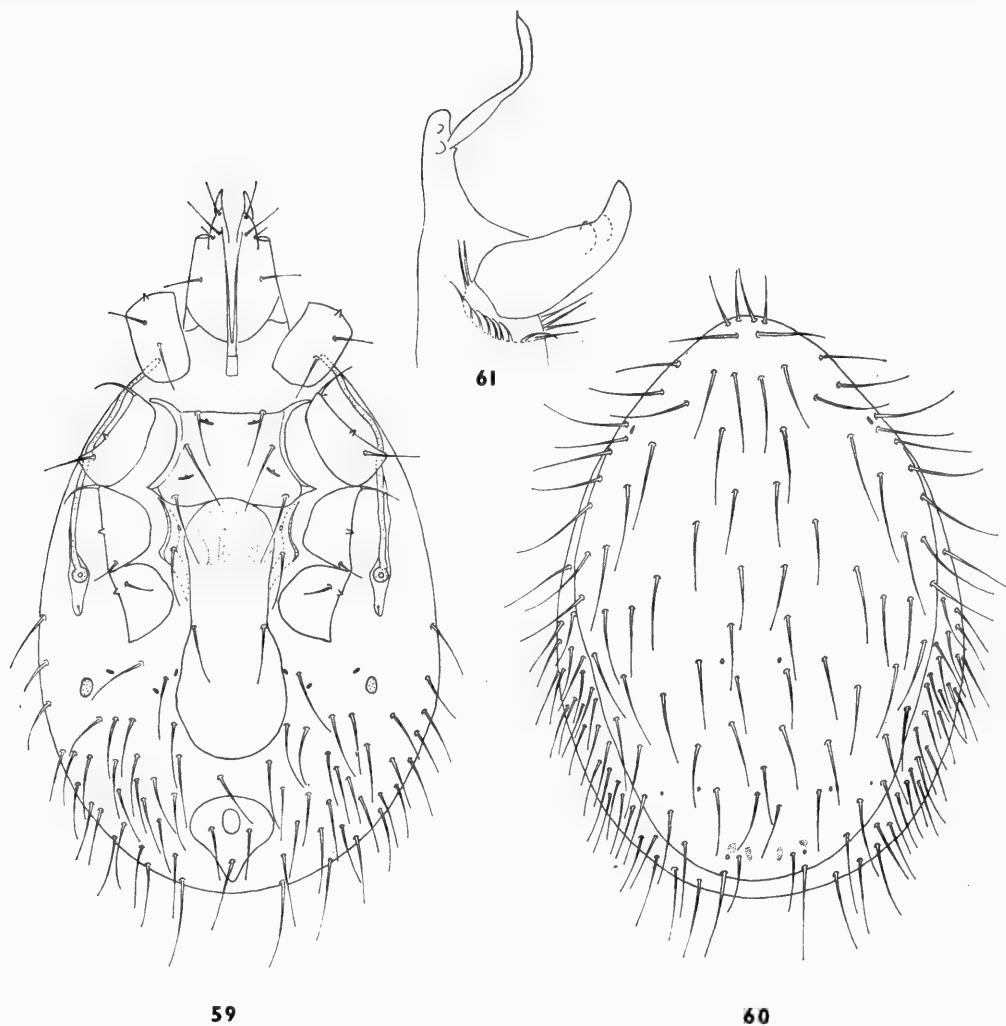
Sternal shield with a reticulate pattern which is most marked antero-laterally. SL=145 μ ; SW=205-214 μ ; SL/SW=0.6-0.7. First sternal seta 1 $\frac{1}{4}$ times as long as metasternal seta, second and third sternal setae a little longer than first.

Genital shield sculptured posteriorly, greatly expanded behind the genital setae. GW₁=247-271 μ ; GW₂=152-170 μ ; GW₁/GW₂=1.5-1.7.

Anal shield approximately as wide as long. AL=143-162 μ ; AW=152-170 μ . Anus situated at approximately its length from the anterior margin. Paranal setae inserted on a level between middle and posterior end of anus, about $\frac{3}{4}$ as long as postanal seta.

Integument of idiosoma bears 26 pairs of marginal and ventral setae, many of which are barbed. Metapodal plates variable in shape, length to width about 2 : 1.

Chaetotaxy of legs normal; anterior and posterior setae on coxa I approximately the same length. Trochanter IV has 2 thick spine-like setae on its anterior surface, and femur IV has a stout ventral seta and a stout dorsal spine. Antero-dorsal seta



FIGS. 59-61. *Androlaelaps georychi* sp. nov., female. Venter (Fig. 59); dorsum (Fig. 60); chelicera (Fig. 61).

on this segment barbed, its length exceeding the width of the femur. Length of tarsus IV about 6 times its width at the base.

MALE (figs. 57-58): Chelicera with an inflated pilus dentilis which tapers distally. Dorsal shield as in female, but setae on central part relatively longer, and 5 accessory setae present between J_3 and J_4 . $DL=694\mu$; $DW=456\mu$; $DL/DW=1.5$. Holoventral shield reticulate, expanded behind coxae IV, bearing 20-21 setae. Chaetotaxy of legs as in female; one ventral seta on femur, genu, tibia and tarsus of leg II stout and spine-like.

HOSTS AND LOCALITIES: *Galago alleni* Waterhouse, Barombikang Forest, British Cameroons (type).

Cricetomys sp., burrow, Kivu, Belgian Congo (M.R.A.C.).

Cricetomys gambianus Waterhouse, Yaoundé, Cameroons (Taufflieb & Mouchet, 1959).

***Androlaelaps georychi* sp. nov.**

FEMALE (figs. 59–61): Deutosternum with 6 rows of 3–4 very fine teeth, a larger median tooth in rows 2 to 4. Hypostomal processes very hairy and large, extending to anterior margin of palp femur. Chelae about 58μ long; pilus dentilis elongate (about 40μ long), moderately inflated; arthrodial filaments subequal in length.

Dorsal shield reticulate, ovoid in shape, widest at level of seta *s*₇. $DL=964-988\mu$; $DW=618\mu$; $DL/DW=1.6$. The shield bears the usual 39 pairs of setae, which are more or less subequal in length, and 5–6 accessory setae in the postero-median region. Lengths of setae *i*₄ and *z*₂ about $1\frac{1}{2}$ times the distance between their bases; seta *Z*₅ $1\frac{1}{2}$ times as long as seta *J*₅.

Sternal shield reticulate; $SL=143-152\mu$; $SW=185-200\mu$; $SL/SW=0.7-0.8$. Genital shield with a reticulate pattern which extends over the anterior flap; greatest width of shield $1.4-1.5$ times width at level of genital setae (GW_2). Length of genital setae about $4/5$ GW_2 .

Anal shield approximately as broad as long. $AL=143-162\mu$; $AW=148-162\mu$. Anus situated at less than its length from the anterior margin of the shield. Paranal setae near posterior margin of anus, extending to a point level with the posterior tip of the anal shield, their length about $\frac{3}{4}$ that of the postanal seta.

Integument of idiosoma bears numerous ventral and marginal setae which all appear to be barbed, except those adjacent to the genital shield. Metapodal plates short, ovoid, length to width not greater than 2 : 1.

Chaetotaxy of legs normal. Length of tarsus IV about 8 times its greatest width. Caruncle IV elongated, its length more than twice the width of tarsus IV and about $1\frac{1}{2}$ times the length of caruncle III.

HOST AND LOCALITY: Four females from *Georychus capensis* (Pallas), Knysna, Cape Province, 24 April, 1954. Holotype and one paratype in the collection of the S.A.I.M.R., Johannesburg, two paratypes (1962.6.12.8–9) in the collection of the British Museum (Natural History).

***Androlaelaps ghanensis* sp. nov.**

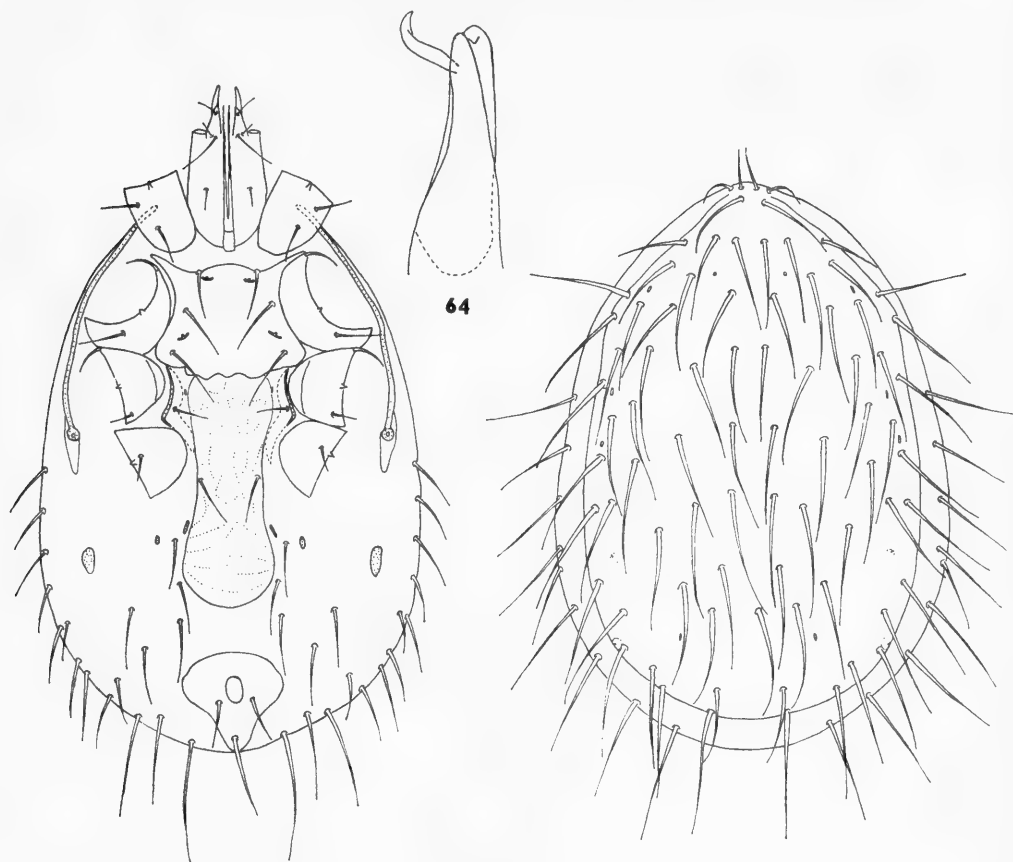
FEMALE (figs. 62–64): Deutosternum with 6 rows of 2–4 teeth. Chelae about 62μ long; pilus dentilis moderately inflated; arthrodial filaments subequal in length.

Dorsal shield reticulate, $817-903\mu$ long, $570-580\mu$ wide at the broadest point, $DL/DW=1.4-1.6$. The shield bears 39 pairs of setae and one unpaired accessory seta at the level of setae *J*₄. All the setae except *i*₁ and *r*₁ are long and thick. Lengths of setae *i*₄ and *z*₂ about twice the distance between their bases; seta *Z*₅ about $1\frac{1}{2}$ times as long as seta *J*₅; seta *J*₁ reaches almost to the base of seta *J*₄.

Sternal shield reticulate, approximately as long as broad; $SL=171-180\mu$;

SW=180 μ . Metasternal setae about 2/3 as long as first pair of sternal setae, second and third pairs of sternal setae slightly longer.

Genital shield widened near its posterior end and with a distinct pattern extending to its anterior margin. GW₁=143-152 μ ; GW₂=105 μ ; GW₁/GW₂=1.4. Genital setae about as long as first pair of sternal setae, slightly shorter than GW₂.



62

63

FIGS. 62-64. *Androlaelaps ghanensis* sp. nov., female. Venter (Fig. 62); dorsum (Fig. 63); chelicera (Fig. 64).

Anal shield as long as broad or slightly longer. AL=157-171 μ ; AW=157 μ ; AL/AW=1.0-1.1. Anus situated at approximately its length from the anterior margin of the shield. Paranal setae level with posterior margin of anus, about 3/5 as long as postanal seta.

Integument of idiosoma bears about 27 pairs of ventral and marginal setae; the marginal and outermost ventral setae are all barbed. Metapodal plates oval in shape, length to width about 5 : 2.

Chaetotaxy of legs normal. Trochanter IV bears two very stout spines, one on the lower ventral and one on the upper dorsal surface. Femur IV bears a stout sword-like basal spine. Length of tarsus IV about 6 times the width at the base.

HOST AND LOCALITY: Four females from a dormouse (*Claviglis* spec.) in Ghana, 1 January, 1911. Holotype (1962.6.12.10) and three paratypes (1962.6.12.11-13) in the collection of the British Museum (Natural History).

Androlaelaps glasgowi (Ewing)

Laelaps glasgowi Ewing, 1925, *Proc. ent. Soc. Wash.* 27 : 6.

Haemolaelaps glasgowi, Strandtmann, 1949, *J. Parasit.* 35 : 343; figs.; Zumpt & Till, 1956, *Z. Parasitenk.* 17 : 282, figs. 1-2.

Laelaps californicus Ewing, 1925, *Proc. ent. Soc. Wash.* 27 : 5.

Laelaps virginianus Ewing, 1925, *Proc. ent. Soc. Wash.* 27 : 6.

Hypoaspis microti Oudemans, 1926; *Ent. Ber.* 7 : 101; Bregetova, 1952, *Zool. Zh.* 31 : 867.

Haemolaelaps mohrae Oudemans, 1928, *Ent. Ber.* 7 : 374.

Haemolaelaps cricetophilus Vitzthum, 1930, *Zool. Jb. Jena, Abt. Syst.* 60 : 417, figs.

Laelaps stegemani Hefley, 1935, *J. Kansas ent. Soc.* 8 : 22.

Ischnolaelaps rhabdomys Radford, 1939, *Parasitology* 31 : 249, fig. 6 (*syn. nov.*).

Haemolaelaps scalopi Keegan, 1946, *Trans. Amer. Micr. Soc.* 65 : 71.

Atricholaelaps sigmodoni Strandtmann, 1946, *J. Parasit.* 32 : 164.

Atricholaelaps strandtmanni Fox, 1947, *Ann. ent. Soc. Amer.* 40 : 580, figs.

Hypoaspis (*Haemolaelaps*) *eos* Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* 14 : 79, fig. 2.

(For further references see Strandtmann & Wharton, 1958, *Manual of Mesostigmatid Mites* : 37)

FEMALE (figs. 65-67): Deutosternum with 6 rows of 3-5 teeth. Chelae about 36μ long; pilus dentilis strongly inflated basally, distal portion slender, curved or recurved; arthrodial filaments usually subequal in length, slightly variable in populations from *Otomys irroratus*.

Dorsal shield reticulate, with a "double" margin. $DL=613-653\mu$; $DW=394-436\mu$; $DL/DW=1.5-1.6$. The shield bears 39 pairs of setae and 2-3 unpaired accessory setae between setae J_2 and J_4 . Lengths of setae i_4 and z_2 slightly exceed the distance between their bases; seta Z_5 about twice as long as J_5 .

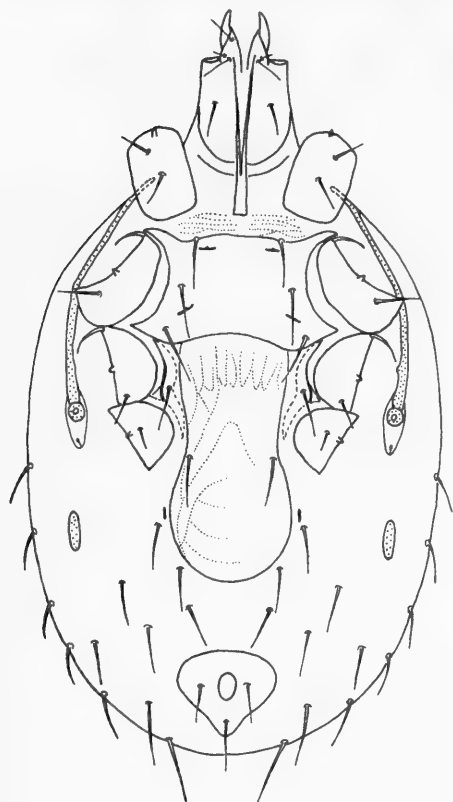
Sternal shield reticulate and granular. $SL=96-113\mu$; $SW=130-155\mu$; $SL/SW=0.75$. Genital shield slightly widened behind genital setae, its reticular pattern extending over the anterior flap. $GW_1=123-140\mu$; $GW_2=96-105\mu$; $GW_1/GW_2=1.2-1.4$. Genital setae relatively short, about half GW_2 .

Anal shield approximately as long as broad. $AL=90-109\mu$; $AW=100-105\mu$. Anus situated at less than its length from the anterior margin; paranal setae level with middle of anus, about $2/3$ as long as postanal seta.

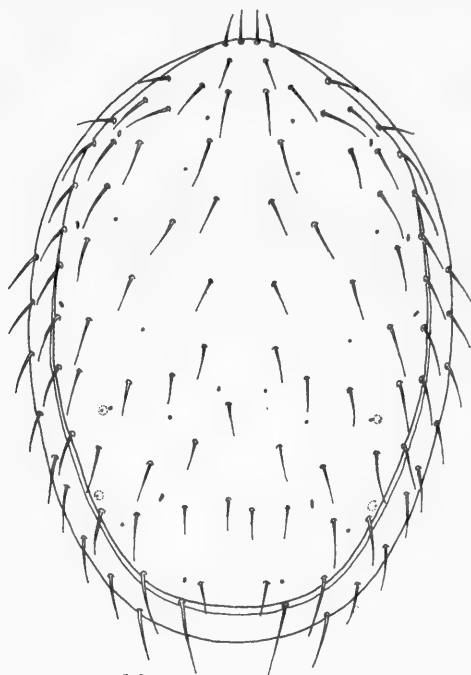
Integument of idiosoma bears 22 pairs of ventral and marginal setae, the latter being a little coarser than the former and provided with fine barbs. Two pairs of ventral setae flank the genital shield. Metapodal plates 3 or 4 times longer than broad.

Chaetotaxy of legs normal; posterior seta on coxa I slightly thicker than anterior seta, but subequal in length. Length of tarsus IV at least 6 times its greatest width.

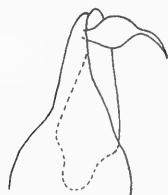
MALE (figs. 68-69): Chelicera as illustrated, pilus dentilis inflated basally. Dorsal shield reticulate, chaetotaxy as in female. $DL=428\mu$; $DW=257\mu$; $DL/DW=1.7$.



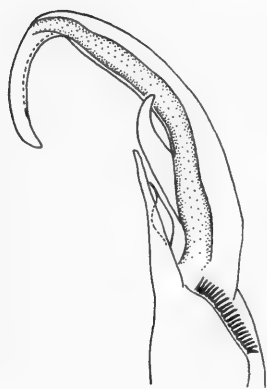
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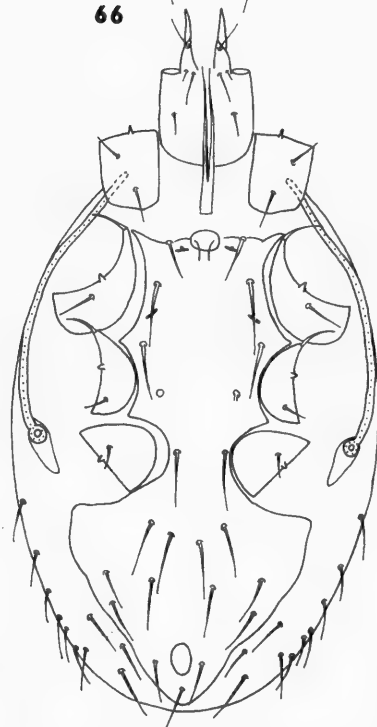
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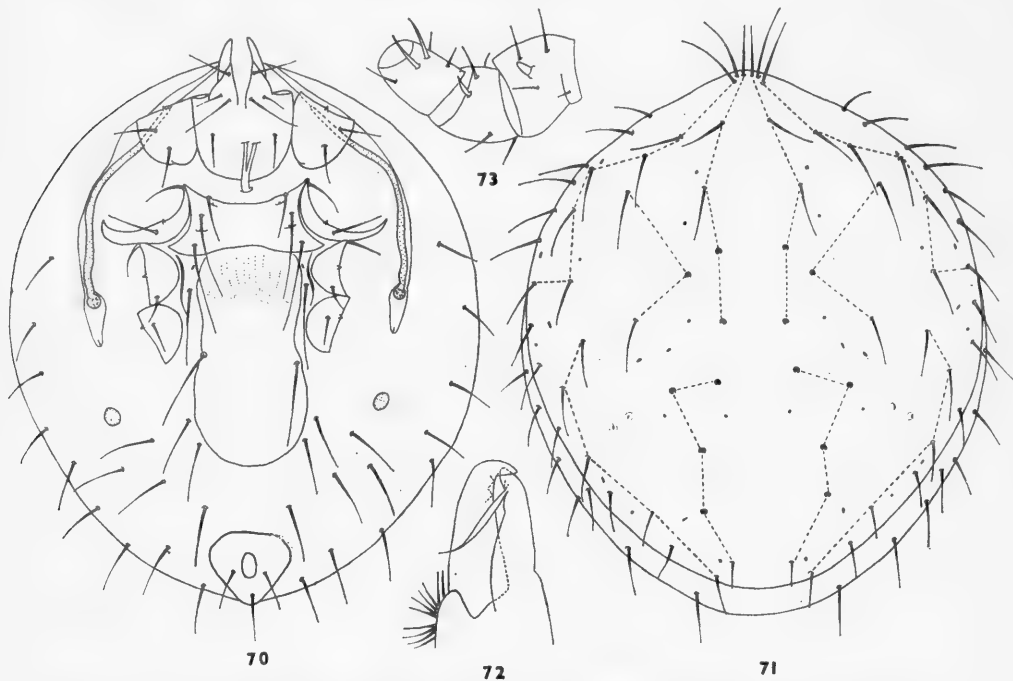


68

FIGS. 65-69. *Androlaelaps glasgowi* (Ewing). Venter (Fig. 65), dorsum (Fig. 66) and chelicera (Fig. 67) of female. Venter (Fig. 68) and chelicera (Fig. 69) of male.

Holovenral shield reticulate, expanded behind coxae IV and bearing 23 setae. Integument with about 14 pairs of ventral and marginal setae. Chaetotaxy of legs as in female.

HOSTS AND LOCALITIES: *Rhabdomys pumilio* (Sparrman) and *Otomys irroratus* (Brants) from several localities in Southern Africa (S.A.I.M.R.; B.M.N.H; types of *I. rhabdomys* in Dr. C. D. Radford's collection).



FIGS. 70-73. *Androlaelaps graingeri* Zumpt & Patterson, female. Venter (Fig. 70); dorsum (Fig. 71); chelicera (Fig. 72); femur, genu, tibia of leg II (Fig. 73).

Androlaelaps graingeri Zumpt & Patterson

Androlaelaps graingeri Zumpt & Patterson, 1952, *J. ent. Soc. S. Afr.* 15 : 162, fig. 2.

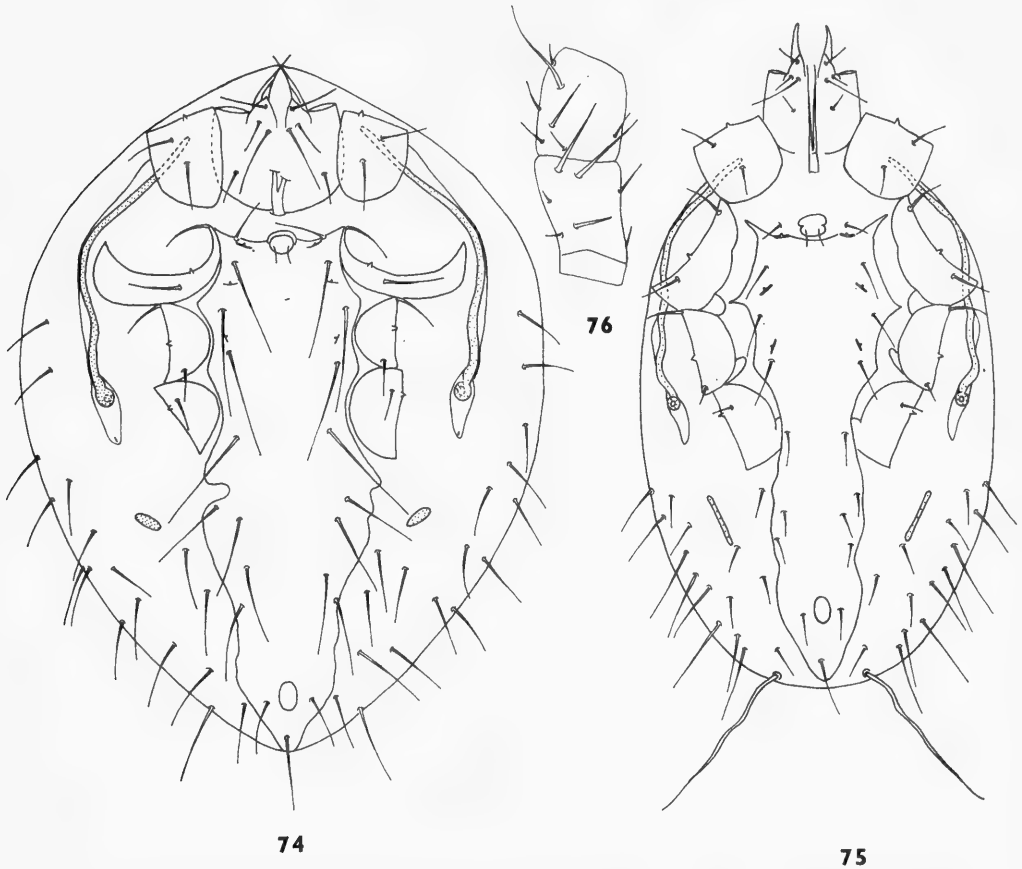
Turkiella graingeri, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 224.

FEMALE (figs. 70-73): Gnathosoma ventral in position in all the specimens examined, only the free segments of the palps extending beyond the anterior margin of the idiosoma. Deutosternum with 6 rows of 3-4 teeth, only one tooth visible in the 5th row. Chelae 74-76 μ long, both digits dentate, movable digit with a pronounced terminal hook which arches over the fixed digit; pilus dentilis slender, arthrodial filaments subequal in length.

Dorsal shield subcircular, with a "double" margin, granular and weakly reticulate. DL=1000-1050 μ ; DW=825-900 μ ; DL/DW=1.2. Chaetotaxy of dorsal shield similar to that of *A. arvicantis*, i.e. setae *px*₂ and *px*₃ missing. Seta *r*₁ considerably longer than seta *i*₁; seta *Z*₅ about twice as long as seta *J*₅; setae *i*₄-*i*₅, *z*₂, *J*₁-*J*₄

rubbed off in all the specimens examined, but are probably subequal with i_3 , as they are in the male. Setae generally finer than in *A. arvicanthis* and apparently without barbs.

Sternal shield with an overall granulation and very weak reticular pattern. $SL=80-96\mu$; $SW=197-228\mu$; $SL/SW=0.4-0.5$. First sternal seta relatively short, 2nd and 3rd sternal and the metasternal setae considerably longer.



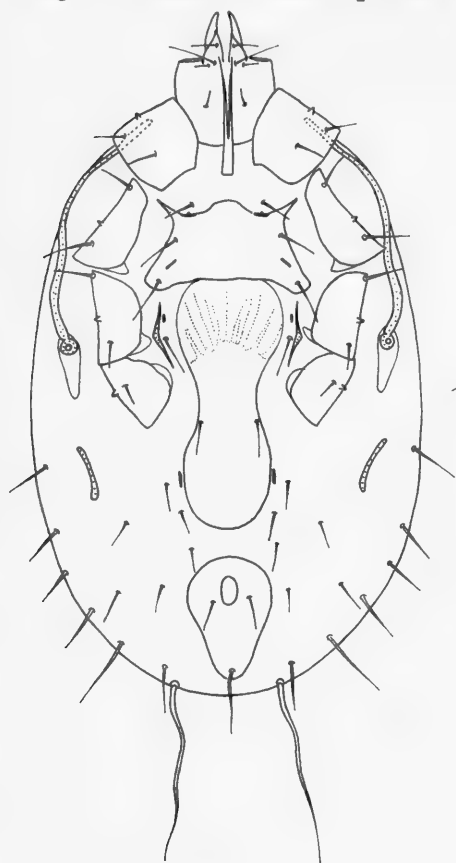
FIGS. 74-76. *Androlaelaps graingeri* Zumpt & Patterson, venter of male (Fig. 74). *Androlaelaps haydocksii* (Till), male. Venter (Fig. 75); dorsal view of femur and genu of leg I (Fig. 76).

Genital shield broadly rounded posteriorly but not greatly expanded behind the genital setae, granular, with a weak reticular pattern. $GW_1=215-236\mu$; $GW_2=188-200\mu$; $GW_1/GW_2=1.1-1.2$. Genital setae relatively long, slightly less than GW_2 , reaching base of second pair of flanking setae.

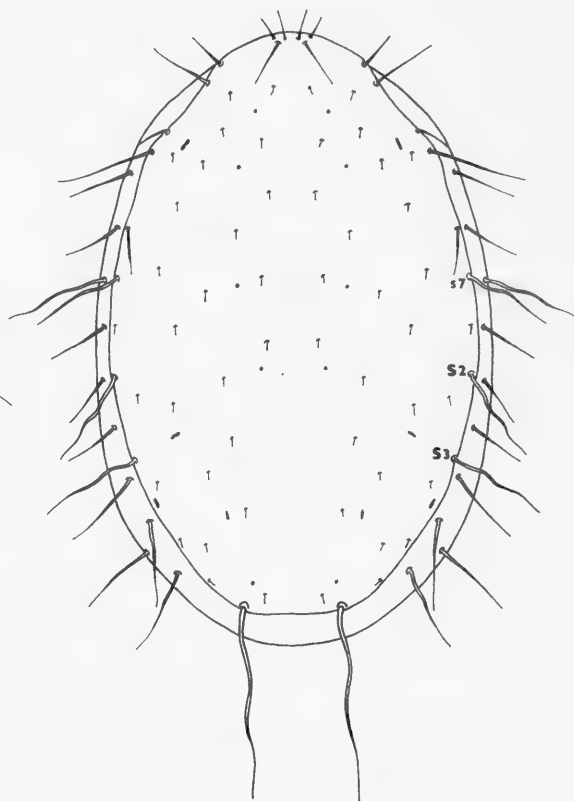
Anal shield reticulate, with a pair of lateral, granular patches; approximately as long as broad. $AL=162-184\mu$; $AW=158-175\mu$. Paranal setae near posterior margin of anus, about $4/5$ as long as postanal seta.

Integument of idiosoma with 21-22 pairs of fine setae. Metapodal plates subcircular.

Chaetotaxy of legs normal. Anterior and posterior setae of coxa I approximately equal in length. Ventral setae on genu and tibia II similar to those in *A. arvicantis*. Length of tarsus IV about $6\frac{1}{2}$ times the width at the base.



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FIGS. 77-78. *Androlaelaps haydocki* (Till), female. Venter (Fig. 77); dorsum (Fig. 78).

MALE (fig. 74): Gnathosoma as in female; spermadactyl about 115μ long. Dorsal shield with chaetotactic pattern similar to that of female; $DL=846\mu$; $DW=646\mu$; $DL/DW=1.3$. Holoventral shield granular with a weak reticular pattern, not expanded behind 4th pair of coxae, bearing 21 setae, of which 4 pairs lie in the preanal region. Metapodal plates oval, length about $2\frac{1}{2}$ times width. Chaetotaxy of legs as in female.

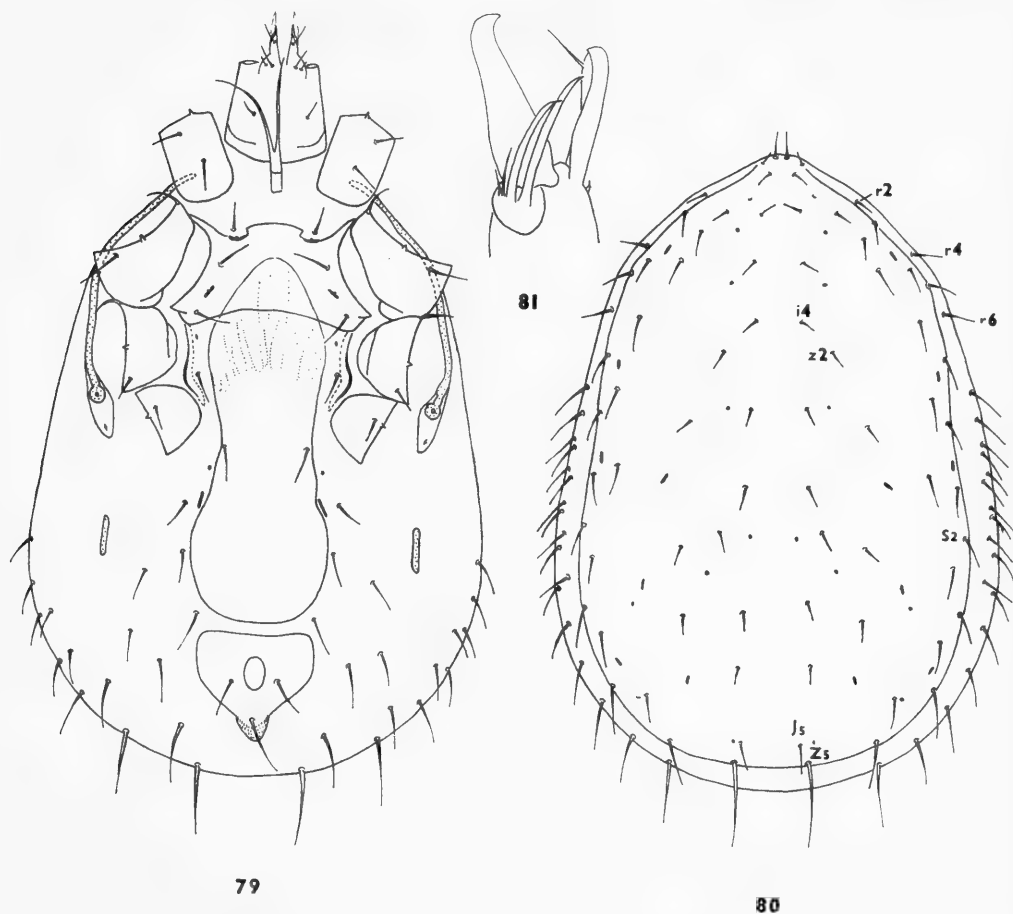
HOST AND LOCALITY: Unidentified rodent, Kerio Valley, Kenya (type series, S.A.I.M.R.).

Androlaelaps haydocki (Till)

Haemolaelaps haydocki Till, 1959, *J. ent. Soc. S. Afr.* 22 : 426, figs.

Androlaelaps haydocki is very closely allied to *A. mesopicos* (Radford) and may prove to be only a subspecies or variety.

FEMALE (figs. 77-78): The female differs from *A. mesopicos* in that the dorsal shield bears 38 pairs of setae, and the marginal setae s_7 , S_2 , and S_3 are long and



FIGS. 79-81. *Androlaelaps heliosciuri* sp. nov., female. Venter (Fig. 79); dorsum (Fig. 80); chelicera (Fig. 81).

sinuous. The genital shield is slightly more expanded posteriorly ($GW_1/GW_2 = 1.3-1.5$), and the anal shield is slightly more elongate ($AL/AW = 1.2-1.4$).

MALE (figs 75-76): The male differs from *A. mesopicos* in having a long dorsal seta on genu I.

HOSTS AND LOCALITIES: *Thripas namaquus* (Lichtenstein), Luanshya (type series) and Muliashi Area, Northern Rhodesia; Debeete, Bechuanaland; Mabelikwa, N.

Transvaal; Mapalane, Mozambique (S.A.I.M.R. and B.M.N.H.).
Campethera abingoni (Smith), Luanshya, N. Rhodesia (B.M.N.H.).

***Androlaelaps heliosciuri* sp. nov.**

FEMALE (figs. 79–81): Deutosternum with 6 rows of 2–3 small teeth; corniculi very weakly sclerotized. Chelae about 40μ long, edentate except for terminal hook on movable digit; pilus dentilis slender; two of the arthrodial filaments considerably longer and thicker than the others.

Dorsal shield reticulate, widest in posterior half at level of seta S2. $DL=618-637\mu$; $DW=385-404\mu$; $DL/DW=1.6$. All 39 pairs of setae are present, but r2, r4 and r6 are off the shield. Lengths of setae i4 and z2 not greater than half the distance between their bases; seta Z5 about 3 times as long as seta J5.

Sternal shield granular, with a faint reticular pattern as well. $SL=76-89\mu$; $SW=128-133\mu$; $SL/SW=0.6-0.7$. First pair of sternal setae situated off the plate, slightly shorter than 2nd and 3rd pairs; metasternal setae as long as 2nd and 3rd pairs of sternal setae.

Genital shield reticulate, the pattern extending over the anterior flap. It is closely approached to the anal shield and widest at the level of the 2nd pair of flanking setae. $GW_1=142-152\mu$; $GW_2=90-95\mu$; $GW_1/GW_2=1.5-1.7$. Genital setae relatively short, less than half GW_2 .

Anal shield broader than long, anterior margin straight. $AL=101-110\mu$; $AW=120-123\mu$; $AL/AW=0.8-0.9$. Paranal setae situated between middle and posterior end of anus, about $2/3$ as long as postanal seta.

Integument of idiosoma bears about 34 pairs of ventral and marginal setae, the former being fine and simple, the latter coarser and barbed. Metapodal plates long and slender, length to width at least 6 : 1.

Chaetotaxy of legs normal. Femur IV bears a stout antero-dorsal seta. Length of tarsus IV about 4 times the width at the base.

HOST AND LOCALITY: Eight females from *Heliosciurus gambianus*, (Ogilby), Amani, Tanganyika, 3 February, 1957. Holotype and three paratypes in the collection of the South African Institute for Medical Research, four paratypes (1962.6.12. 14–17) in the collection of the British Museum (Natural History).

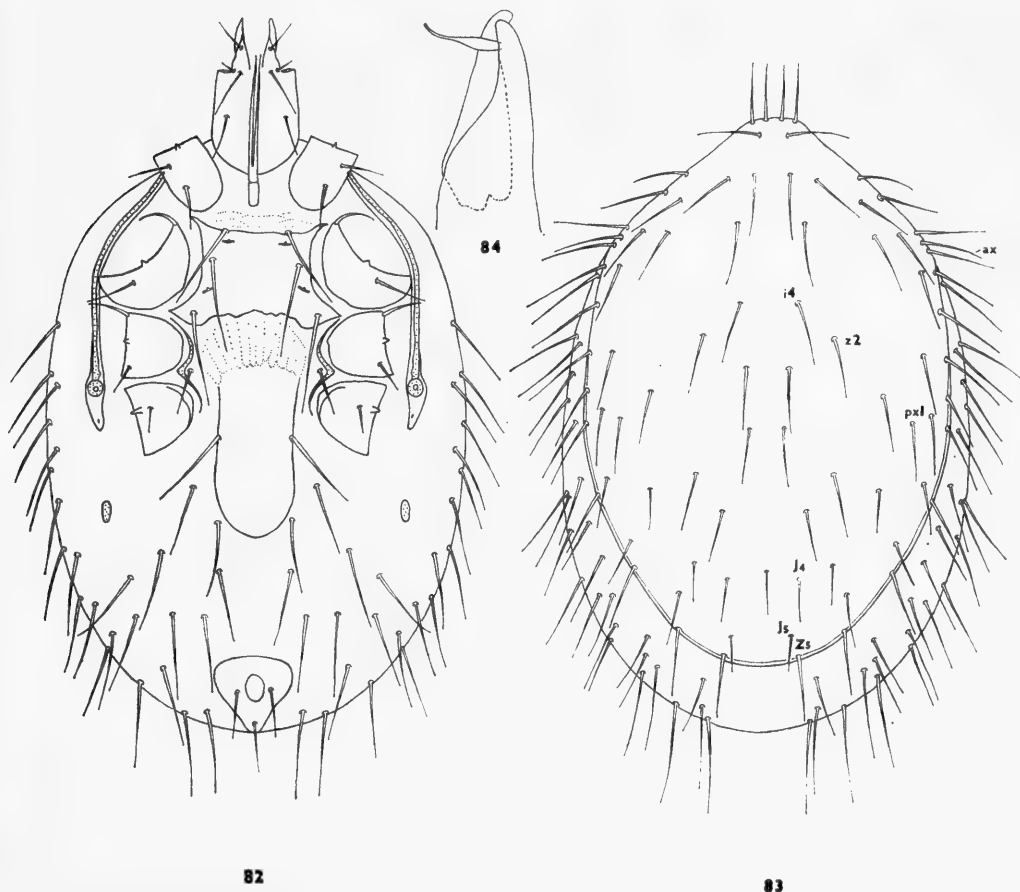
***Androlaelaps hirsti* (Keegan)**

Haemolaelaps hirsti Keegan, 1956, *J. Egypt. publ. Hlth. Ass.* 31 : 242, figs. 26–30; Costa, 1961, *Bull. Brit. Mus. (nat. Hist.) Zool.* 8 : 14, figs. 17–20.

FEMALE (figs. 82–84): Deutosternum with 6 rows each of 4 small teeth, except the last row which has 3 teeth. Chelae about 80μ long; pilus dentilis inflated basally, tapering distally; arthrodial filaments subequal in length.

Dorsal shield ovoid, with a "double" margin, widest about the middle, tapering posteriorly, granular in appearance with faint reticulations. $DL=1092-1188\mu$; $DW=703-817\mu$; $DL/DW=1.4-1.6$. The shield bears 41 pairs of setae, one pair being present in the ax and one pair in the px1 position. One of the specimens

examined has an unpaired accessory seta between setae J_4 ; the remaining specimens have no accessory setae. The setae on the central part of the shield are relatively long, the lengths of i_4 and z_2 exceeding the distance between their bases. The posterior terminal setae Z_5 are approximately the same length as setae i_4 and at least $2\frac{1}{2}$ times as long as setae J_5 .



FIGS. 82-84. *Androlaelaps hirsti* (Keegan), female. Venter (Fig. 82); dorsum (Fig. 83); chelicera (Fig. 84).

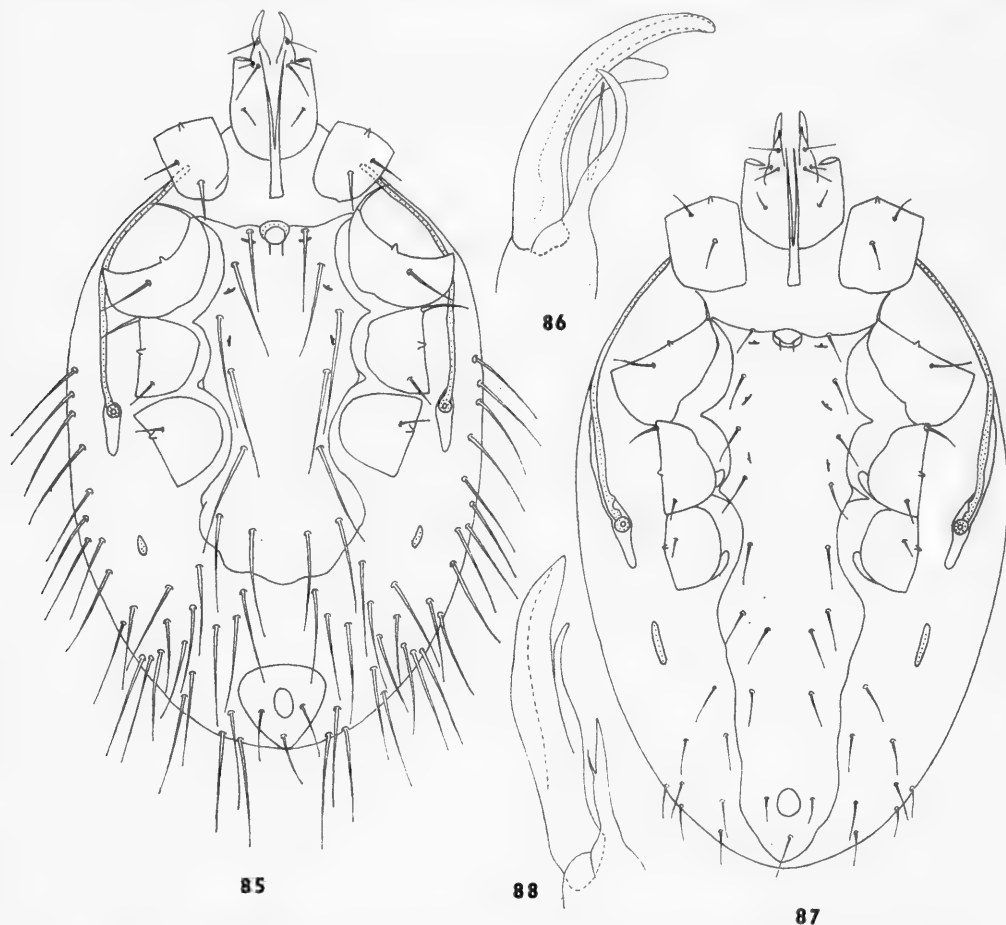
Sternal shield granular with a faint reticulate pattern, presternal area reticulate and slightly granular. $SL=162-180\mu$; $SW=225-257\mu$; $SL/SW=0.6-0.8$. Sternal setae long, first pair reaching posterior margin of shield, third pair reaching middle of coxae IV; metasternal seta about half as long as second sternal seta.

Genital shield granular, not expanded posteriorly; $GW_2=162-180\mu$. Genital setae relatively long, reaching base of second pair of flanking setae, their length nearly equal to GW_2 .

Anal shield as long as, or slightly longer than, broad. $AL=175-190\mu$; $AW=$

162–175 μ ; AL/AW=1.0–1.2. Anus less than its length from the anterior margin of the shield. Paranal setae inserted on a level between middle and posterior margin of anus, extending beyond base of postanal seta, and slightly longer than this seta.

Integument of idiosoma with numerous long marginal and ventral setae, many of the former being barbed. Metapodal plates oval, length about twice breadth.



FIGS. 85–88. *Androlaelaps hirsti* (Keegan), venter (Fig. 85) and chelicera (Fig. 86) of male.

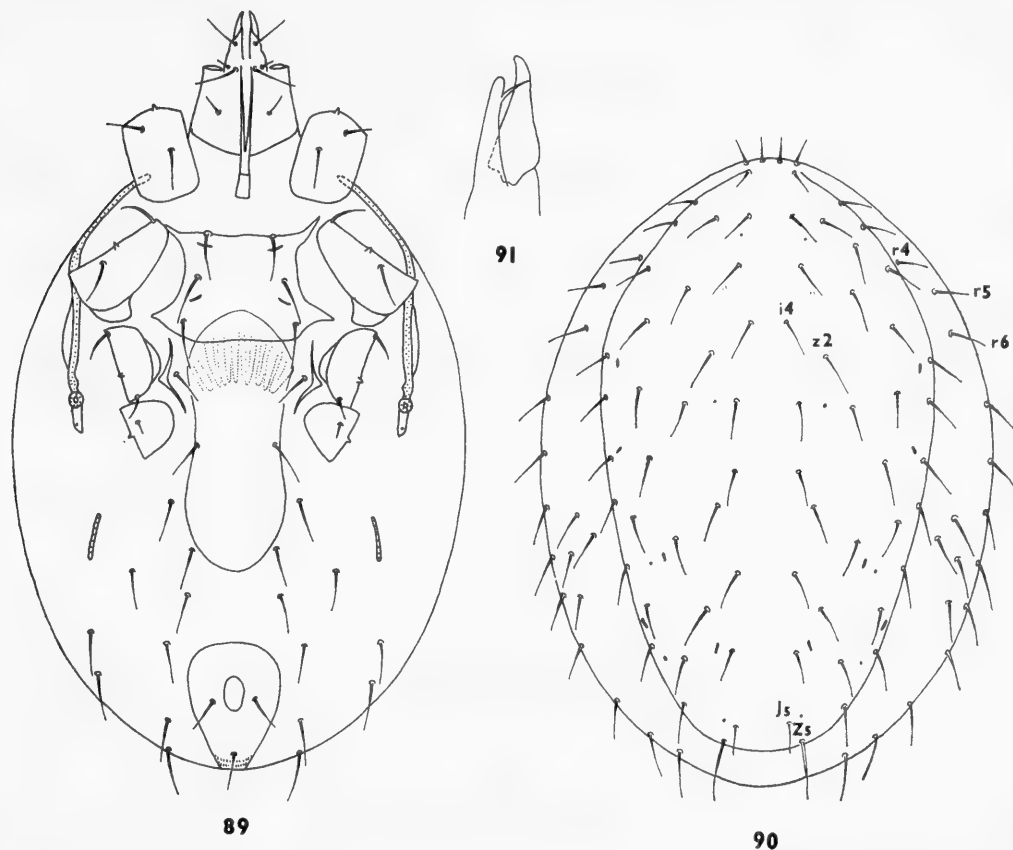
Androlaelaps hystrici (Zumpt & Till), venter (Fig. 87) and chelicera (Fig. 88) of male.

Tibia III has 9 setae instead of the usual 8. Ventral setae on coxa I nearly equal in length but posterior seta much thicker. Two short, stout, spur-like setae on femur I; one stout ventral seta on genu II, two on tibia II, 3 stout ventral and 3 stout apical setae on tarsus II, two of the apical ones being relatively blunt. Length of tarsus IV is 7–8 times its width at the base.

MALE (figs. 85–86): Fixed digit of chelicera with a long slender pilus dentilis.

Deutosternum with 6 rows of 2 or 3 teeth. Dorsal shield as in the female, but the setae are relatively longer. Anal shield separated from the sternito-ventral shield which bears 7 pairs of setae, 2 pairs being situated on the part posterior to coxae IV. Chaetotaxy of legs as in the female.

HOSTS AND LOCALITIES: Unidentified rat from Yubo, Equatoria, Sudan (Paratype in B.M.N.H.). The above description is based on specimens from *Gerbillus pyramidum* Geoffroy from Israel, received by courtesy of Dr. M. Costa.



FIGS. 89-91. *Androlaelaps hystrici* (Zumpt & Till), female. Venter (Fig. 89); dorsum (Fig. 90); chelicera (Fig. 91).

Androlaelaps hystrici (Zumpt & Till)

Haemolaelaps hystrici Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 235, figs. 12-16; Keegan, 1956, *J. Egypt. publ. Hlth. Ass.* 31 : 239, fig. 23.

FEMALE (figs. 89-91): Deutosternum with 6 rows each of 3 teeth. Chelae 34μ long; pilus dentilis slender; arthrodistal filaments subequal in length. Anterior rostral seta at least $1\frac{1}{2}$ times as long as capitular seta.

Dorsal shield ovoid, posterior margin almost straight. $DL=600-662\mu$; $DW=$

290–362 μ ; DL/DW=1.8–2.3. Only 36 pairs of setae are present on the shield, r4–r6 being inserted on the adjacent integument. Setae simple, of moderate length; lengths of i4 and z2 about $\frac{3}{4}$ the distance between their bases; seta Z5 at least $1\frac{1}{2}$ times as long as seta J5.

Sternal shield reticulate. SL=93–114 μ ; SW=103–134 μ ; SL/SW=0.8–1.0. Setae relatively short, first seta reaching base of second.

Genital shield slightly granular, with a few indistinct traces of a reticulate pattern, very slightly widened behind genital setae, then tapering. GW₁=93–103 μ ; GW₂=83–93 μ . Length of genital setae about half GW₂.

Anal shield pear-shaped. AL=93–134 μ ; AW=93–103 μ ; AL/AW=1.0–1.3. Anus situated at approximately its length from the anterior margin. Paranal setae inserted on a level between middle and posterior end of anus and approximately as long as the postanal seta.

Integument of idiosoma bears about 22 pairs of ventral and marginal setae, of which two pairs border the genital shield. Metapodal plates extremely narrow, length to width about 10 : 1.

Chaetotaxy of legs normal. Posterior seta on coxa I slightly longer than anterior seta. Legs relatively slender; length of tarsus IV 8 times the width at the base.

MALE (figs. 87–88): Fixed digit of chelicera with a slender pilus dentilis. Dorsal shield ovoid, 500 μ long and 263 μ wide; DL/DW=1.9. Chaetotaxy as in the female, except that r4–r6 are inserted on the shield. Holovenral shield narrow, bearing 19 setae. Metapodal plates broader than in the female. Chaetotaxy of legs as in female, but some of the setae relatively stouter, for example, femur II has two broad, spine-like ventral setae, tibia II has one very broad, spear-like ventral seta, tarsus II has two broad, spine-like, ventral setae, but the apical setae are slender.

HOSTS AND LOCALITIES: *Hystrix cristata* Linnaeus from Karamoja district, Uganda (type series in S.A.I.M.R. and B.M.N.H.) and from Njoro, Rift Valley Province, Kenya (Keegan, 1956).

Keegan (1956) records this species from *Arvicanthis niloticus* (Desmarest) and *Rattus rattus* (Linnaeus) in Egypt, and also an additional specimen, which should probably be referred to this species, from *Crocidura manni* Peters, Kano, Nigeria.

Androlaelaps longipes (Bregetova)

Haemolaelaps longipes Bregetova, 1952, *Zool. Zh.* 31 : 867, figs.; Costa, 1961, *Bull. Brit. Mus. (nat. Hist.) Zool.* 8 : 21, figs. 28–32.

Haemolaelaps namrui Radford, 1954, *Fieldiana, Zool.* 34 : 310, figs. 56–57 (*syn. nov.*).

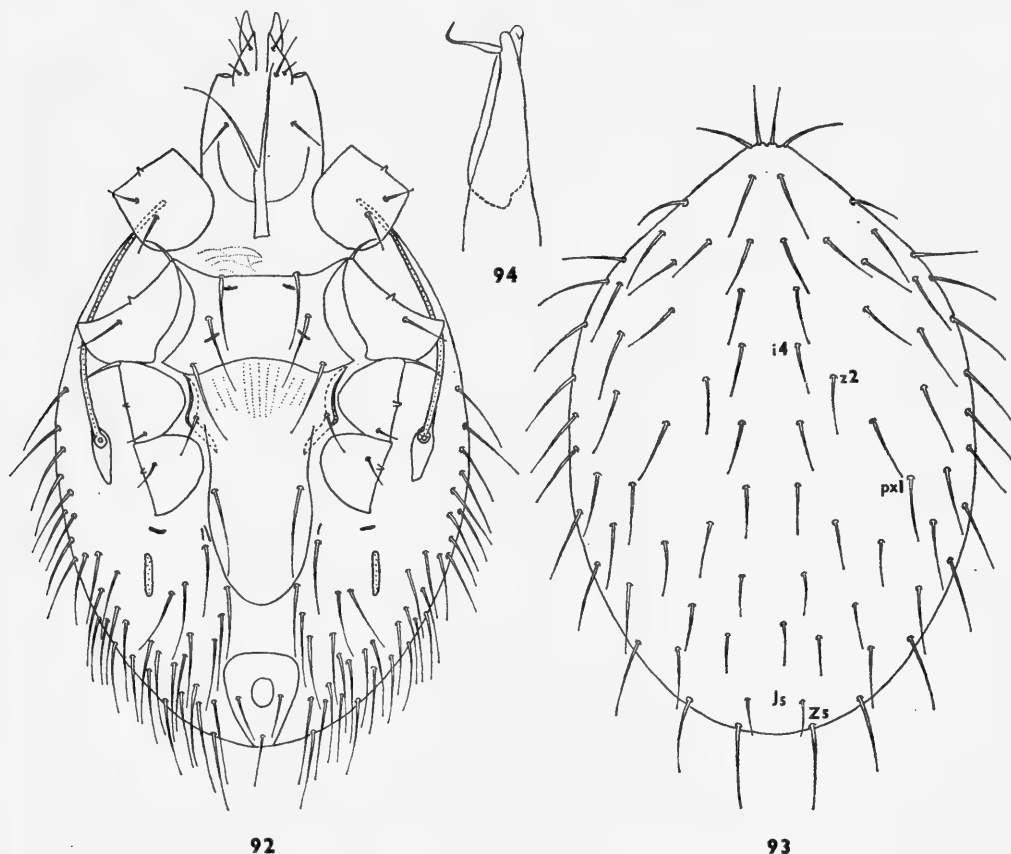
Haemolaelaps aegyptius Keegan, 1956, *J. Egypt. publ. Hlth. Ass.* 31 : 246, figs. 37–38.

FEMALE (figs. 92–94): Deutosternum with 6 rows of 3–4 small teeth. Chelae about 55 μ long; pilus dentilis slightly inflated basally, distal $2/3$ slender; arthrodial filaments subequal in length.

Dorsal shield ovoid, with a reticulate pattern. DL=703 μ ; DW=475 μ ; DL/DW=1.5. The shield bears 40 pairs of setae, one pair being present in the *pxi* position on the posterior half of the shield. There is also an unpaired seta near the mid-line

between setae J_3 and J_4 . The setae on the central part of the shield are relatively long, the lengths of i_4 and z_2 being approximately equal to the distance between their bases. The anterior and marginal setae are longer, some of the longest setae having fine barbs. Seta Z_5 is more than twice as long as seta J_5 .

Sternal shield reticulate. $SL=95\mu$; $SW=147\mu$; $SL/SW=0.7$. Sternal setae long, the first pair reaching almost to the posterior margin of the shield, second and



FIGS. 92-94. *Androlaelaps longipes* (Bregetova), female. Venter (Fig. 92); dorsum (Fig. 93); chelicera (Fig. 94).

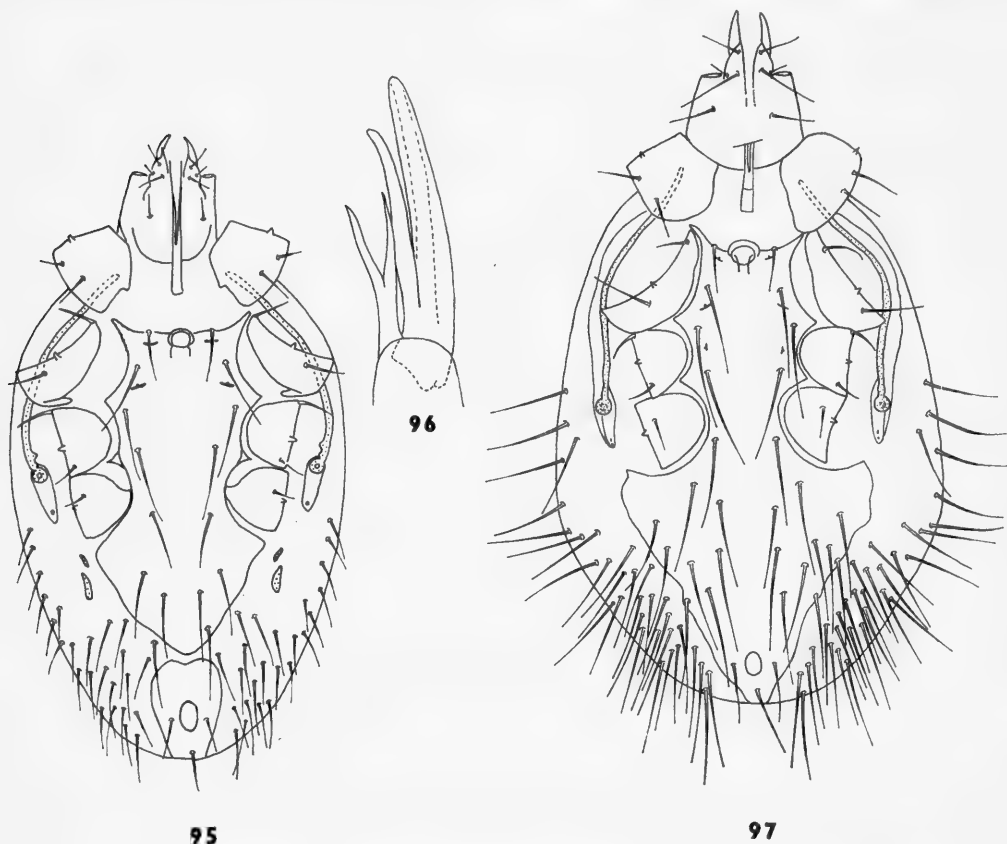
third pairs slightly longer, the 3rd pair extending well beyond the bases of the metasternal setae. Metasternal seta less than half as long as 3rd sternal seta.

Genital shield with a reticulate pattern, slightly widened behind genital setae, then tapering posteriorly. $GW_1=125\mu$; $GW_2=120\mu$. Genital setae relatively long, about $9/10$ GW_2 , extending to base of second pair of flanking setae.

Anal shield slightly longer than wide, anterior margin straight. Length (to base of postanal seta) is 103μ , greatest width is 98μ . Anus approximately equidistant between anterior margin of shield and postanal seta. Paranal setae situated between middle and posterior margin of anus, about the same length as the postanal seta.

Integument of idiosoma bears about 37 pairs of apparently simple ventral and marginal setae, of which 2 pairs flank the genital shield. Metapodal plates elongate, 7 times as long as broad.

Chaetotaxy of legs normal except that tibia III has 9 setae. Posterior seta on coxa I is $1\frac{1}{2}$ times as long and thick as anterior seta. Stout ventral setae are present on the femur, genu, tibia and tarsus of leg II, three of the terminal setae on tarsus II are stout and blunt. The dorsal seta on trochanter IV is much thicker than the



FIGS. 95-97. *Androlaelaps longipes* (Bregetova), venter (Fig. 95) and chelicera (Fig. 96) of male.

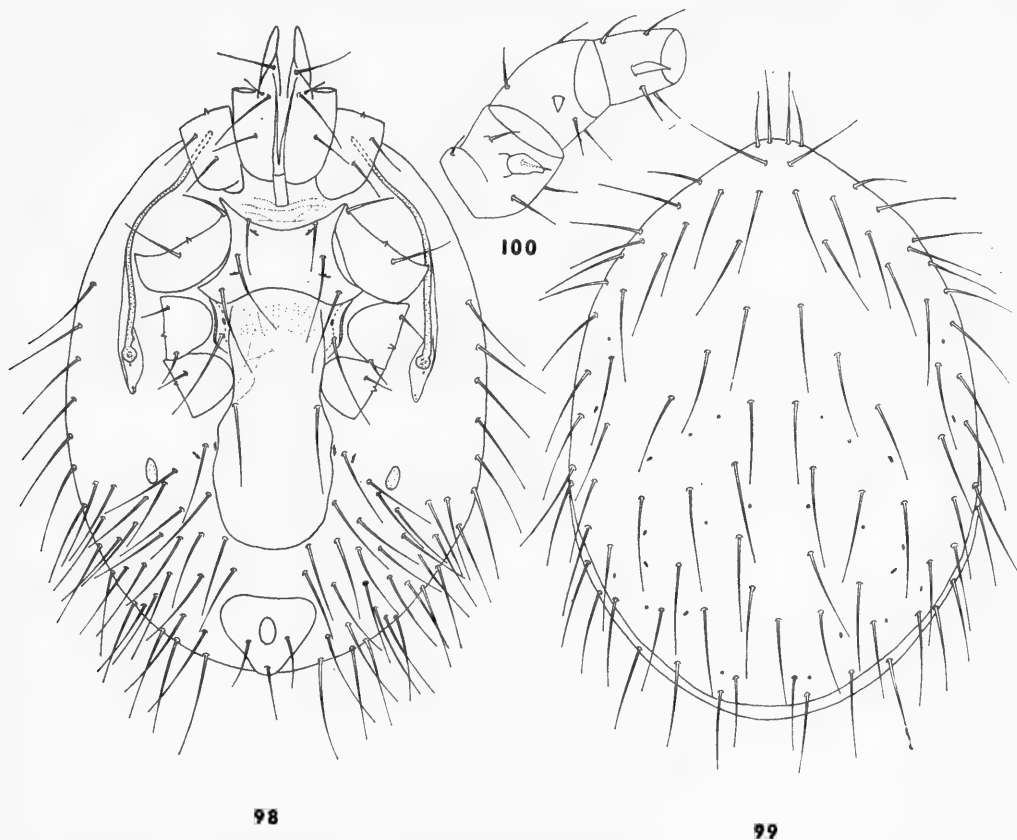
Androlaelaps marshalli Berlese, venter of male (Fig. 97).

other setae on this segment. Length of tarsus IV about 8 times the width at the base.

MALE (figs. 95-96): Fixed digit of chelicera (in *A. longipes* from the U.S.S.R.) bears a large, tapering pilus dentilis. Dorsal shield similar to that of female. Holoventral shield divided into a sternito-ventral shield and a separate anal shield. The sternito-ventral shield is moderately expanded behind the 4th pair of coxae and bears 7-8 pairs of setae, 2 or 3 pairs being situated on the part posterior to

coxae IV. The ventral shield is more reduced in the Russian specimen than in the type specimen of *A. namrui*, on which the description and drawings are based. Integument of idiosoma bears about 31 pairs of setae. Chaetotaxy of legs as in the female.

HOSTS AND LOCALITIES: *Meriones rex* Yerbury & Thomas, Ta'izz, Yemen (types of *A. namrui* in Dr. C. D. Radford's collection).



FIGS. 98-100. *Androlaelaps marshalli* Berlese, female. Venter (Fig. 98); dorsum (Fig. 99); ventral view of femur, genu and tibia of leg II (Fig. 100).

Bregetova (1952) recorded *A. longipes* from *Meriones* species in the U.S.S.R. (material in B.M.N.H.).

Keegan's specimens (*A. aegyptius*) were collected from a variety of hosts at several localities in Egypt, and Costa (1961) has found this species chiefly on *Meriones* species in Israel.

Androlaelaps marshalli Berlese

Laelaps (Androlaelaps) marshalli Berlese, 1911, *Redia* 7 : 429.

Androlaelaps marshalli, Keegan, 1956, *J. Egypt. publ. Hthl Ass.* 31 : 227, fig. 13; Costa, 1961, *Bull. Brit. Mus. (nat. Hist.) Zool.* 8 : 45, figs. 75-79.

Hypoaspis (Androlaelaps) africanus Zumpt, 1950, *Parasitology* 40 : 30, fig. 2.

Turkiella africanus, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 216.

Hypoaspis (Androlaelaps) africanoides Zumpt & Patterson, 1950, *S. Afr. J. med. Sci.* 15 : 72, figs. 2-3.

Androlaelaps oudemansi Radford, 1944, *Parasitology* 35 : 161, fig. 2 (syn. nov.).

Turkiella oudemansi, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 224.

FEMALE (figs. 98-100): Deutosternum with 6 rows of teeth, 3 to 6 small, finely pointed teeth in each row. Chelae similar to those of *A. arvicanthis*, 70-90 μ long; pilus dentilis slender; arthrodial filaments subequal in length.

Dorsal shield with a "double" margin and an overall reticular pattern. DL=863-1050 μ ; DW=675-763 μ ; DL/DW=1.2-1.5. The shield bears 39 pairs of setae as well as additional unpaired setae between J_3 and J_4 . Many of the setae are barbed. Lengths of setae i_4 and z_2 slightly exceed the distance between their bases; seta Z_5 only slightly longer than J_5 .

Sternal shield with a well-defined reticular pattern and with concave anterior and posterior margins. SL=88-123 μ ; SW=180-193 μ ; SL/SW=0.5-0.6. First sternal seta reaches second pore, second and third sternal and metasternal setae distinctly longer.

Genital shield broadly rounded posteriorly, with an overall reticular pattern. $GW_1=228-250\mu$; $GW_2=150-175\mu$; $GW_1/GW_2=1.4-1.6$. Genital setae relatively long, approximately equal to GW_2 , and extending almost to the base of the second pair of flanking setae.

Anal shield with a reticular pattern; anus at slightly less than its length from the anterior margin; paranal setae situated near posterior half of anus, only slightly shorter than postanal seta. AL=123-166 μ ; AW=150-175 μ ; AL/AW=0.8-1.0.

Integument of idiosoma bears 30-55 pairs of long ventral and marginal setae, most of which are barbed. Metapodal plates oval, length about twice the breadth.

Chaetotaxy of legs normal, except that the type of *A. oudemansi* and some of the other specimens assigned to this species have 9 setae on tibia III instead of the usual eight. Anterior and posterior setae on coxa I approximately equal in length. Thorn-like seta on femur II relatively large; inner ventral seta on genu II short and spine-like. Inner ventral seta on tibia II a little shorter and considerably stouter than the outer seta in the types of *A. oudemansi* and *A. africanoides*, whereas in specimens previously identified as *A. africanus* the differences between these two setae are less striking, as in *A. arvicanthis*. Tarsus II bears 3 stout, blunt, terminal setae. Length of tarsus IV about 8 times its width at the base.

MALE (fig. 97): Deutosternum as in female; chelicera similar to that of *A. arvicanthis*. Dorsal shield similar to that of the female. DL=890-980 μ ; DW=570-608 μ ; DL/DW=1.6. Holoventral shield strongly reticulate, expanded behind fourth pair of coxae, and bears 23-31 setae. The number of setae between coxae IV and the anus is 10-19, but there may be more on one side than on the other. Chaetotaxy of legs as in the female.

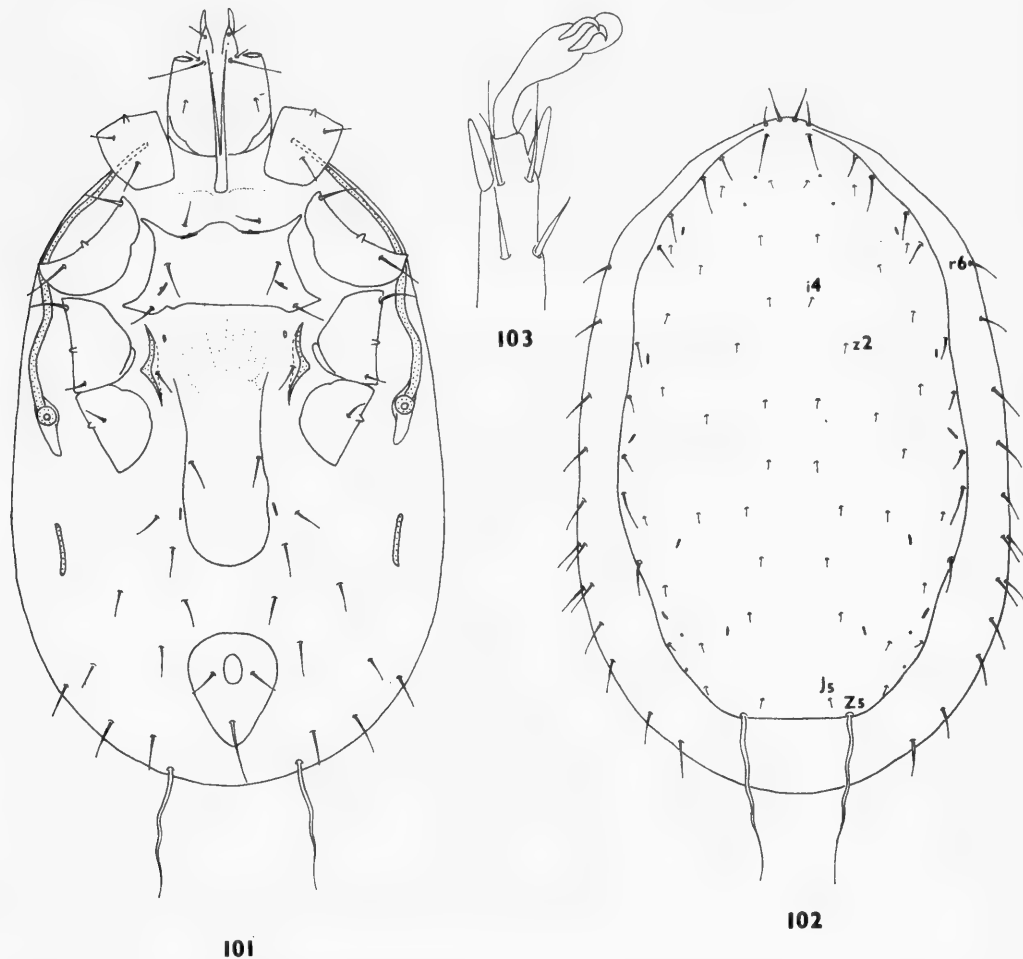
HOSTS AND LOCALITIES: Recorded in Southern Africa from the following hosts (Zumpt & Till, 1961):—

Tatera afra (Gray), *Gerbillus paebe* Smith, *Desmodillus auricularis* (Smith), *Rattus paedulcus* (Sundevall), *Rattus natalensis* (Smith), *Rattus chrysophilus* (De Winton),

Rattus namaquensis (Smith), *Rhabdomys pumilio* (Sparrman), *Lemniscomys griselda* (Thomas), *Saccostomus campestris* Peters, *Steatomys pratensis* Peters, *Pedetes capensis* (Forster), *Cryptomys hottentotus* (Lesson) and *Oryctolagus cuniculus* (Linnaeus).

Specimens from the following East African hosts have been examined:—

Arvicanthis niloticus (Desmarest), Bunyoro, Uganda (type of *A. oudemansi* in B.M.N.H.).



FIGS. 101–103. *Androlaelaps mesopicos* (Radford), female. Venter (Fig. 101); dorsum (Fig. 102); tip of tarsus IV, ventral view (Fig. 103).

Tatera valida (Bocage), Bunyoro, Uganda (S.A.I.M.R.).

Tatera nigricauda Peters, Lali Hills, Kenya (S.A.I.M.R.).

Tatera species, W. Nile District, Uganda (S.A.I.M.R.).

Taterillus emini (Thomas), W. Nile District, Uganda (S.A.I.M.R.).

Tachyoryctes splendens (Rüppell), Muguga, Kenya (S.A.I.M.R.).

Unidentified rodent, Kerio Valley, Kenya (S.A.I.M.R.).

A. marshalli has also been recorded from an unidentified rodent in the Sudan and from gerbils in Egypt (Keegan, 1956) and from gerbils in Israel (Costa, 1961).

Two series of mites which have been provisionally assigned to *A. marshalli* have been obtained from carnivores, namely, *Suricata suricatta* (Schreber) from Queens-town, Cape Province (S.A.I.M.R.), and *Ictonyx striatus* (Perry) from Muguga, Kenya (S.A.I.M.R.).

The drawings of *A. marshalli* are based on paratypes of *A. africanoides* from *Tatera afra* (Gray), S. Rhodesia.

Androlaelaps mesopicos (Radford)

Haemolaelaps mesopicos Radford, 1942, *Parasitology* 34 : 192, figs. 14-19; Till, 1959, *J. ent. Soc. S. Afr.* 22 : 423, figs.

Hypoaspis (Haemolaelaps) mesopicos, Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* 14 : 72.

A series of mites from *Mesopicos griseocephalus*, Natal, has been assigned to this species (Till, 1959). Although differing slightly from the types, especially in the male sex, these mites probably represent no more than a form or variety of *A. mesopicos*.

FEMALE (figs. 101-103): Deutosternum provided with 6 rows of 2-4 small teeth. Chelae about 40 μ long; pilus dentilis small, inflated; arthrodistal filaments subequal in length.

Dorsal shield oval in shape, truncate posteriorly, with a reticulate pattern. DL=700-735 μ ; DW=420-438 μ ; DL/DW=1.6-1.7. Not more than 37 pairs of setae can be distinguished on the shield, seta *s*₃ being absent and seta *r*₆ arising from the integument adjacent to the shield. Seta *px*₃ is present in the type but absent in the specimens from Natal. The marginal setae are variable in size, the longest of the *S* setae being more than 3 times as long as the *J* setae. Seta *Z*₅ is sinuous and whip-like and about 20 times as long as seta *J*₅. The setae on the median part of the shield (*i*₂-*i*₅, *J* series, *z* series, *Z*₁-*Z*₄, *s*₂-*s*₆) are very minute, subequal, the lengths of setae *i*₄ and *z*₂ being less than a quarter the distance between their bases.

Sternal shield granular, presternal area weakly reticulate. SL=84-105 μ ; SW=152-158 μ ; SL/SW=0.6-0.7. First pair of sternal setae slightly shorter than second and third pairs, and lying on the presternal area. Metasternal setae as long as the 2nd and 3rd sternal setae.

Genital shield slender, weakly reticulate posteriorly; GW₁=96-144 μ ; GW₂=80-96 μ ; GW₁/GW₂=1.1-1.3. Genital setae relatively short, less than half GW₂.

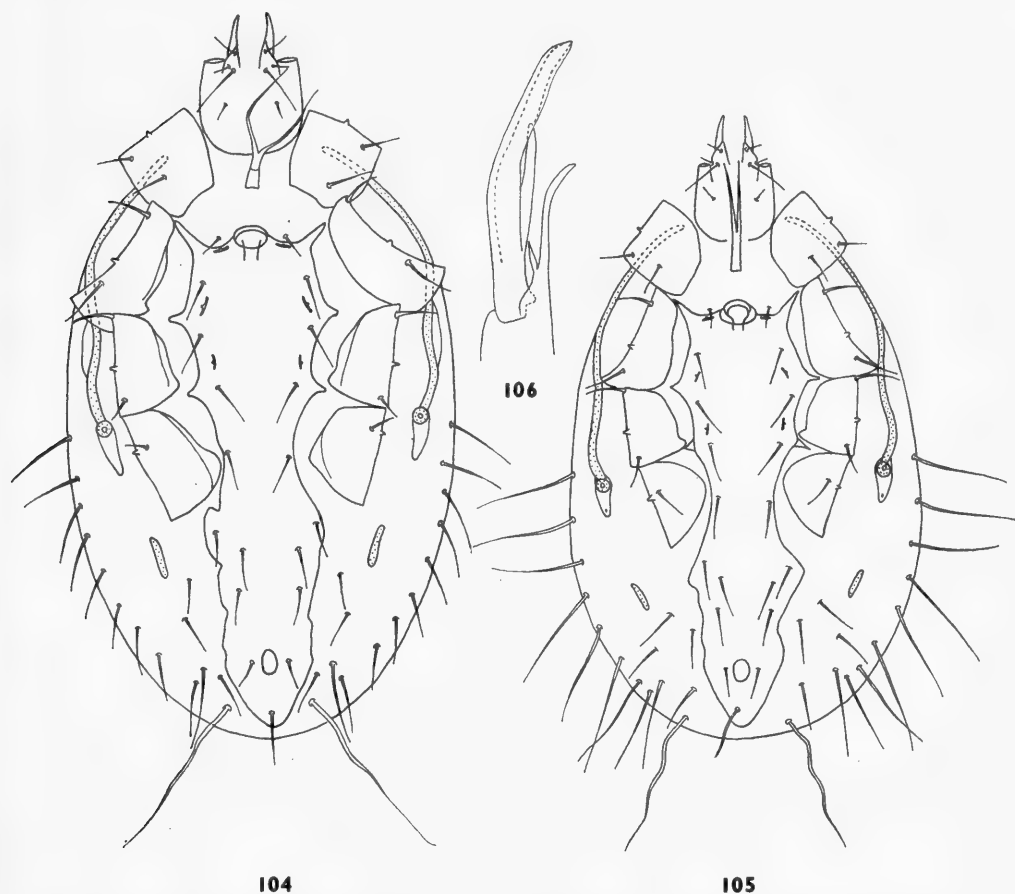
Anal shield pear-shaped with a reticular pattern antero-laterally, relatively shorter and broader in the specimens from Natal. AL=123-150 μ ; AW=96-105 μ ; AL/AW=1.2-1.6. Paranal setae level approximately with middle of anus, not more than 2/3 as long as postanal seta.

Integument of idiosoma bears about 23 pairs of marginal and ventral setae, which all appear to be simple, except for the long, sinuous, posterior terminal pair. Metapodal plates slender, slightly curved.

Tibia III bears 9 setae and tarsi II, III and IV each bear two stout, blunt,

terminal spines. The anterior and posterior setae on coxa I are approximately equal in length and thickness. Length of tarsus IV about 4 times the width at the base.

MALE (figs. 104-106): Fixed digit of chelicera with a small setiform structure near its base. Dorsal shield reticulate, and also granular in the specimen from Natal; shape and chaetotaxy as in the female, the marginal setae, however, being



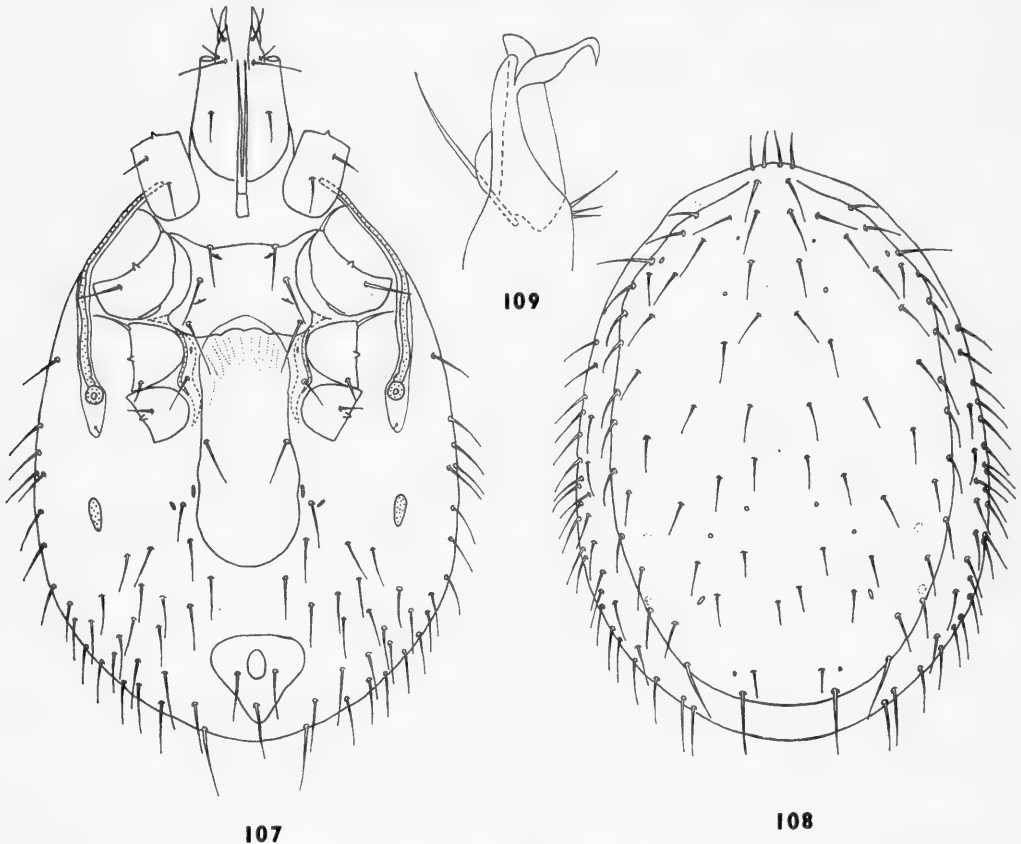
FIGS. 104-106. *Androlaelaps mesopicos* (Radford), male. Venter of type specimen from Uganda (Fig. 104); venter (Fig. 105) and chelicera (Fig. 106) of specimen from Natal.

considerably longer. In the type, setae S_2 and S_3 , and in the Natal specimen S_4 also, are long and sinuous. $DL=618-646\mu$; $DW=350-360\mu$; $DL/DW=1.6-1.7$. Holoventral shield bears 19 setae. Sternal region similar in shape to sternal shield of female, with a granular appearance and faint reticular markings; reticular pattern more distinct on remaining part of shield. Posterior to coxae IV the shield is narrow with irregular margins.

Integument of idiosoma bears about 16 pairs of marginal and ventral setae, the

posterior pair being long and sinuous as in the female. In the specimen from Natal the longest marginal setae are approximately twice as long as in the type specimen. Metapodal plates as in the female.

The legs bear the same number of setae as in the female, but there are modifications in the form of some of the setae. On femur II, the lower medio-ventral seta is modified to form a thickened spur. Tarsi II, III and IV each bear one stout, terminal spine, and tarsus II has, in addition, two blunt ventral spurs.



FIGS. 107-109. *Androlaelaps murinus* (Berlese), female. Venter (Fig. 107); dorsum (Fig. 108); chelicera (Fig. 109).

HOSTS AND LOCALITIES: *Mesopicos griseocephalus ruwenzori* Sharpe, Kabale, Uganda (types in B.M.N.H.).

Mesopicos g. griseocephalus (Boddaert), Pietermaritzburg, Natal (S.A.I.M.R. and B.M.N.H.).

Androlaelaps murinus (Berlese)

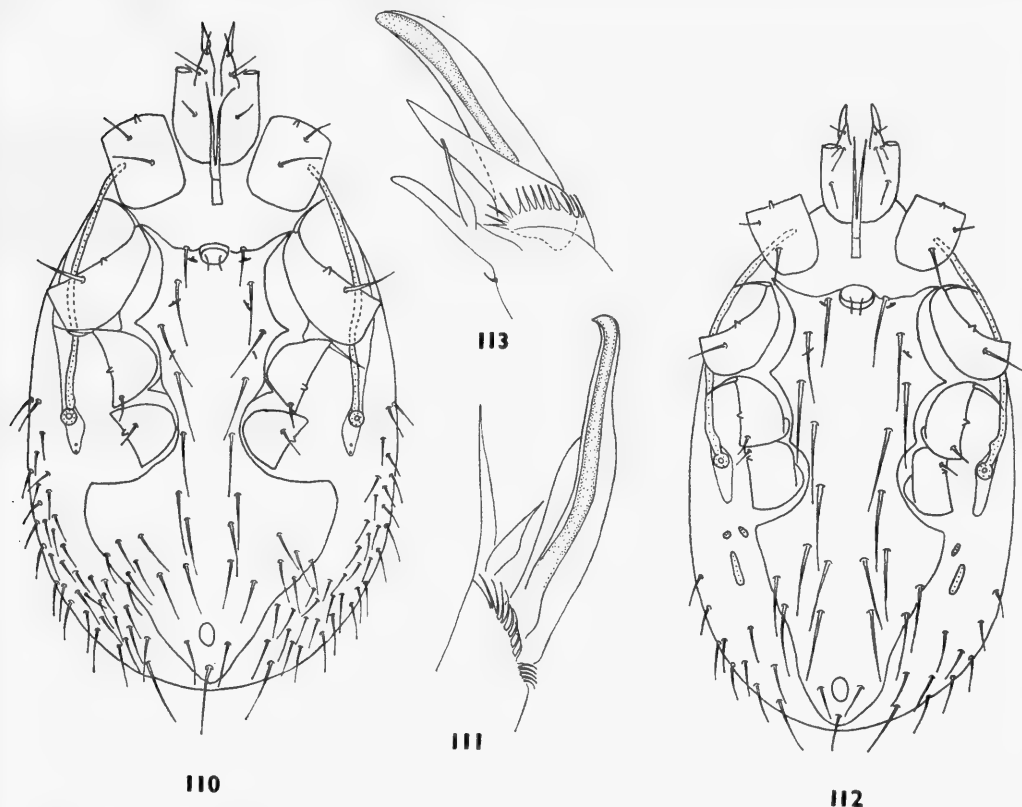
Laelaps (*Haemolaelaps*) *murinus* Berlese, 1911, *Redia* 7 : 432.

Haemolaelaps murinus, Keegan, 1956, *J. Egypt. publ. Hlth. Ass.* 31 : 233, figs. 16-17.

Ischnolaelaps arvicantis Radford, 1939, *Parasitology* 31 : 246, fig. 3.

FEMALE (figs. 107–109): Deutosternum provided with 6 rows of 3–4 teeth. Chelae 52–54 μ long, movable digit with a pronounced terminal hook which arches over the fixed digit; pilus dentilis strongly inflated basally, terminal portion slender, curved; one of the arthrodistal filaments strikingly longer than the others.

Dorsal shield ovoid; DL=860–912 μ ; DW=595–648 μ ; DL/DW=1.4–1.5. The shield bears 39 pairs of setae and 2–3 unpaired accessory setae. Lengths of setae



FIGS. 110–113. *Androlaelaps murinus* (Berlese), venter (Fig. 110) and chelicera (Fig. 111) of male.

Androlaelaps oliffi (Zumpt & Patterson), venter (Fig. 112) and chelicera (Fig. 113) of male.

*i*₄ and *z*₂ a little less than the distance between their bases; seta *Z*₅ about twice as long as seta *J*₅.

Sternal shield strongly reticulate; SL=120–140 μ ; SW=166–184 μ ; SL/SW=0.7–0.8. Metasternal setae shorter than first pair of sternal setae.

Genital shield slightly widened posteriorly and having a reticulate pattern which extends over the anterior flap. GW₁=184–210 μ ; GW₂=128–140 μ ; GW₁/GW₂=1.4–1.5. Length of genital setae about half GW₂.

Anal shield approximately as long as broad; AL=145–150 μ ; AW=145–160 μ .

Anus a little less than its length from the anterior margin; paranal setae inserted slightly behind middle of anus, a little shorter than the postanal seta.

Integument of idiosoma bears about 60 pairs of setae of which about 15 pairs are truly ventral in position. The marginal setae tend to be stouter than the ventral ones and have fine barbs.

Chaetotaxy of legs normal. Anterior seta on coxa I $3/4$ as long as posterior seta; dorsal seta on trochanter IV stout and spine-like; two of the dorsal setae on femur IV spine-like. Length of tarsus IV about 7 times its width at the base.

MALE (figs. 110-111): The chelicerae have the structure indicated in the figure. Holoventral shield reticulate, expanded behind coxae IV, bearing 31-32 setae. Integument of idiosoma bears numerous setae. Chaetotaxy of dorsal shield and legs as in the female. $DL=665\mu$; $DW=437\mu$; $DL/DW=1.5$.

HOSTS AND LOCALITIES: *Arvicanthus niloticus* (Desmarest) from Uganda (type of *I. arvicanthus* in B.M.N.H.) and from Kenya (Keegan, 1956).

Otomys species, Uganda (B.M.N.H.).

Otomys irroratus (Brants) and *Rattus natalensis* (Smith) from Southern Rhodesia (S.A.I.M.R.).

Oenomys hypoxanthus (Pucheran) from the Belgian Congo (B.M.N.H.) and from the Cameroons (I.R.S.C.).

Dasymys incommisus (Sundevall) from Kampala, Uganda (S.A.I.M.R.) and from the Rift Valley Province, Kenya (Keegan, 1956).

Rhabdomys pumilio (Sparrman), *Lophuromys flavopunctatus* Thomas and *Lemniscomys striatus* (Linnaeus) from the Rift Valley Province, Kenya (Keegan, 1956).

Androlaelaps oliffi (Zumpt & Patterson)

Hypoaspis (*Haemolaelaps*) *oliffi* Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* 14 : 81, fig. 3.

Haemolaelaps oliffi, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 243.

FEMALE: (figs. 114-116): Deutosternum with 6 rows of 2-4 teeth. Chela 38-40 μ long; pilus dentilis slightly inflated; arthrodial filaments subequal in length.

Dorsal shield ovoid, reticulate. $DL=620-644\mu$; $DW=368-410\mu$; $DL/DW=1.5-1.7$. The shield bears the usual 39 pairs of setae; lengths of setae 14 and 22 slightly exceed the distance between their bases; seta Z5 is $1\frac{1}{3}$ times as long as seta J5.

Sternal shield reticulate; $SL=96-105\mu$; $SW=130-135\mu$; $SL/SW=0.7-0.8$. Metasternal setae slightly shorter than first pair of sternal setae.

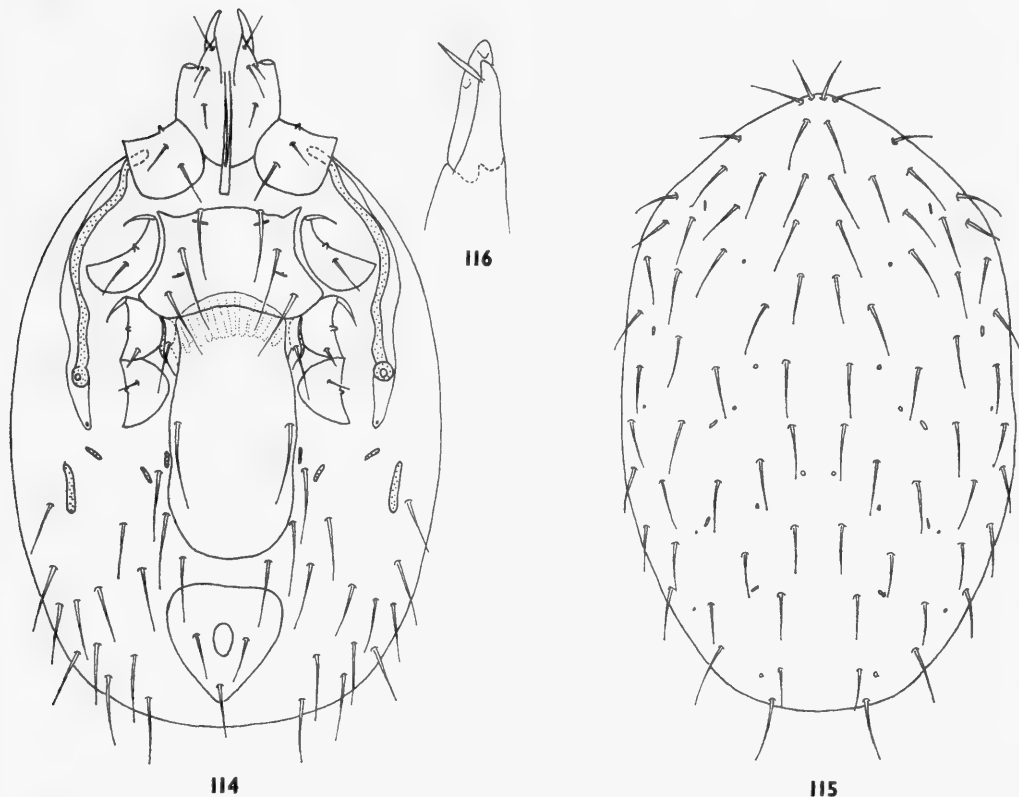
Genital shield granular and with a reticulate pattern which extends over the anterior flap. The shield is not expanded behind the genital setae, GW_1 and GW_2 both varying between 127 μ and 135 μ . Length of genital setae about $2/3$ GW_2 .

Anal shield approximately as long as broad, or slightly longer; $AL=123\mu$; $AW=114-118\mu$. Anus situated at about $1\frac{1}{2}$ times its length from the anterior margin. Paranal setae level approximately with middle of anus, almost reaching base of postanal seta. Postanal seta about the same length as the paranal setae, but slightly thicker.

Integument of idiosoma bears 15 pairs of setae, of which 3 pairs border the

genital shield; some marginal setae are barbed. Metapodal plates slender, length to width about 7 : 1.

Chaetotaxy of legs normal except that tibia III bears 9 setae. Posterior seta on coxa I nearly twice as long and thick as anterior seta. Anterior seta on coxa II and both setae on coxa III rather stout. Three of the apical setae on tarsus II are stout and one of these is blunt. Length of tarsus IV about $5\frac{1}{2}$ times the width at the base.



FIGS. 114-116. *Androlaelaps oliffi* (Zumpt & Patterson), female. Venter (Fig. 114); dorsum (Fig. 115); chelicera (Fig. 116).

MALE (figs. 112-113): Chelicera as figured; dorsal shield reticulate, chaetotaxy as in the female; DL = $428-437\mu$; DW = 276μ ; DL/DW = 1.6. Holoventral shield reticulate, bearing 23 setae; these, excluding the anals, are longer and stouter than those of the integument. Integument bears about 16 pairs of ventral and marginal setae; metapodal plates elongate. Chaetotaxy of legs as in the female.

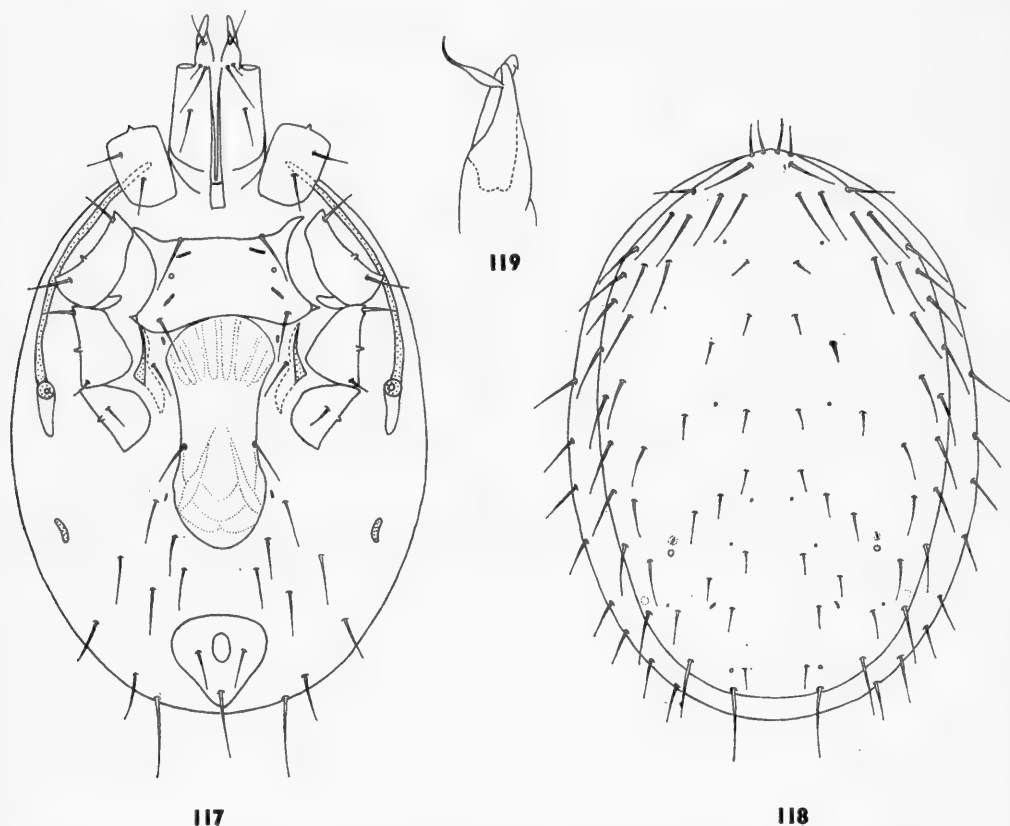
HOSTS AND LOCALITIES: Widely distributed in Southern Africa, mainly on *Tatera afra* (Gray) and *Gerbillus paeba* Smith, and occasionally found on *Saccostomus campestris* Peters and *Desmodillus auricularis* (Smith) (S.A.I.M.R., B.M.N.H. and M.R.A.C.). Found also in Tanganyika on *Tatera afra* (Gray) (B.M.N.H.).

Androlaelaps pachyptilae (Zumpt & Till)

Haemolaelaps pachyptilae Zumpt & Till, 1956, *Z. Parasitenk.* 17 : 285, fig. 3.

FEMALE (figs. 117-119): Deutosternum with 6 rows each of 3-4 small teeth. Chelae 40μ long; pilus dentilis inflated basally, distal half slender and curved; arthrodistal filaments subequal in length.

Dorsal shield ovoid, reticulate, widest between setae *r7* and *s7*. DL= $604-691\mu$;



FIGS. 117-119. *Androlaelaps pachyptilae* (Zumpt & Till), female. Venter (Fig. 117); dorsum (Fig. 118); chelicera (Fig. 119).

DW= $385-446\mu$; DL/DW= $1.5-1.6$. The shield bears 39 pairs of setae. Those on the central part of the shield are relatively short, the lengths of setae *i4* and *z2* being about half the distance between their bases. The anterior and marginal setae are considerably longer; seta *Z5* is barbed and is about $2\frac{1}{2}$ times as long as seta *J5*.

Sternal shield with a reticulate pattern, which is more pronounced antero-laterally, the central part of the shield having a granular appearance. Presternal

area strongly reticulate. $SL=79-100\mu$; $SW=140-158\mu$; $SL/SW=0.5-0.7$. First sternal seta nearly $1\frac{1}{2}$ times as long as metasternal seta.

Genital shield short, slightly widened behind genital setae and then tapering posteriorly; a reticulate pattern is present posteriorly but is not very sharply defined. $GW_1=100-114\mu$; $GW_2=92-96\mu$; $GW_1/GW_2=1.1-1.2$. Genital setae the same length as the ventral setae which flank the shield, about half GW_2 .

Anal shield slightly wider than long. $AL=105-114\mu$; $AW=114-123\mu$; $AL/AW=0.9$. Anus situated at less than its length from the anterior margin. Paranal setae level with middle of anus, not more than $2/3$ as long as postanal seta. Length of postanal seta almost equal to its distance from the anterior margin of the shield.

Integument of idiosoma bears 16 pairs of ventral and marginal setae, two pairs bordering the genital shield and a third pair lying between the genital and anal shields. The marginal setae are mostly barbed, the ventral ones simple. Metapodal plates elongate, length to width about 4 : 1.

Chaetotaxy of legs normal. Posterior seta on coxa I slightly longer than anterior seta. Length of tarsus IV about 5 times the width at the base.

MALE: Not known.

HOST AND LOCALITY: *Pachyptila desolata* (Gmelin) from Heard Island (type series in S.A.I.M.R.).

Androlaelaps patersoni (Zumpt & Till)

Haemolaelaps patersoni Zumpt & Till, 1956, *Z. Parasitenk.* 17 : 286, fig. 4.

FEMALE (figs. 120-122): Deutosternum with 6 rows of 3-6 very fine teeth. Chelae $42-46\mu$ long; pilus dentilis spatulate, terminating in a short, fine, slightly bent point; arthrodial filaments subequal in length.

Dorsal shield bears 39 pairs of setae and a variable number (5-12) of unpaired accessory setae which may extend anterior to setae *i5*. Lengths of setae *i4* and *z2* approximately equal to the distance between their bases; seta *Z5* at least twice as long as seta *J5*. $DL=683-753\mu$; $DW=420-481\mu$; $DL/DW=1.5-1.6$.

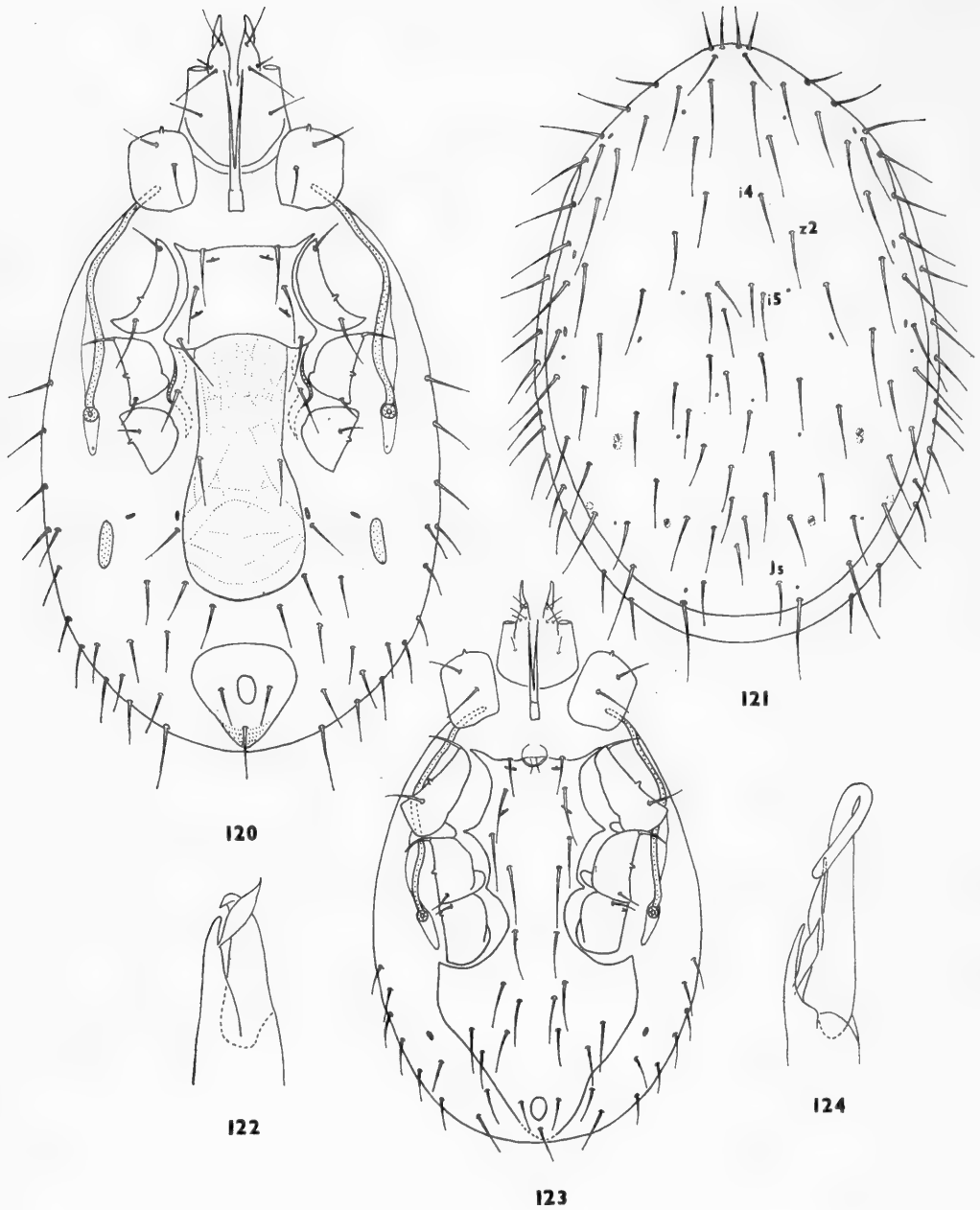
Sternal shield reticulate; $SL=100-114\mu$; $SW=130-149\mu$; $SL/SW=0.7-0.8$. Metasternal setae a little shorter than first pair of sternal setae.

Genital shield moderately expanded posteriorly, with a reticulate pattern extending over the anterior flap. $GW_1=135-154\mu$; $GW_2=96-114\mu$; $GW_1/GW_2=1.3-1.5$. Length of genital setae at least half GW_2 .

Anal shield with an overall reticulate pattern; $AL=114-131\mu$; $AW=127-131\mu$; $AL/AW=0.9-1.0$. Anus situated at approximately its length from the anterior margin of the shield. Paranal setae level with middle of anus, about $4/5$ as long as postanal seta.

Integument bears about 30 pairs of setae. Outer metapodal plates elongate, length to width 4-5 : 1. Chaetotaxy of legs normal. Anterior and posterior setae on coxa I subequal in length and thickness. Length of tarsus IV about 7 times the width at the base.

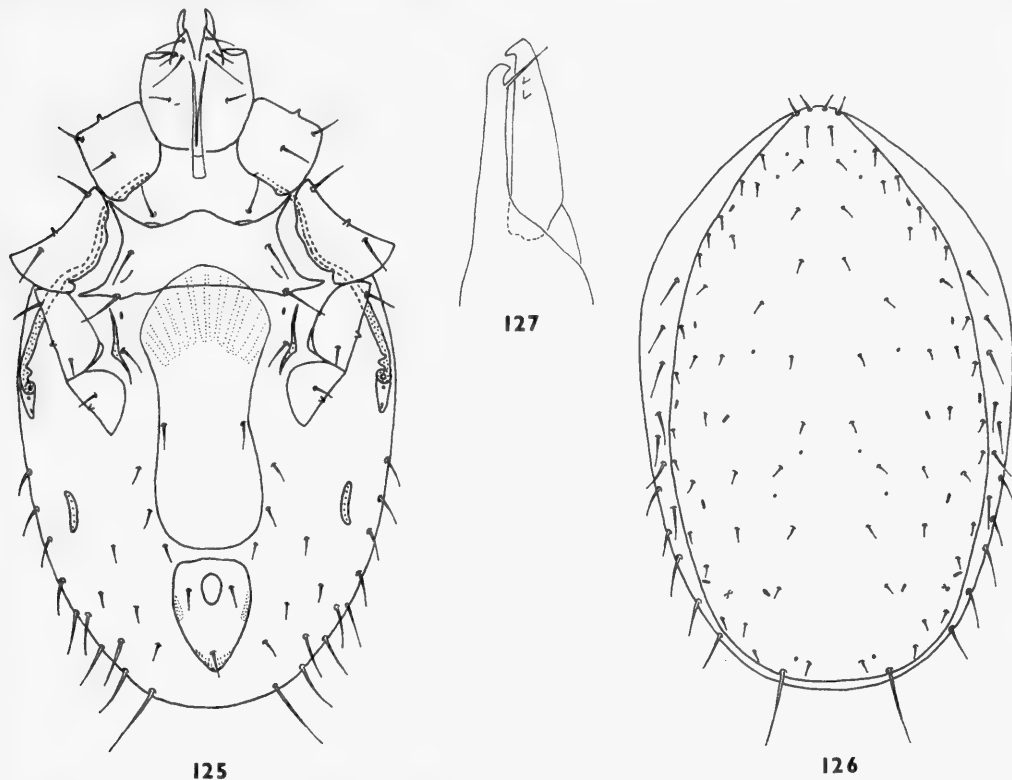
MALE (figs. 123-124): The chelicerae have the structure shown in the figure, the fixed digit bearing a pilus dentilis similar to that of the female.



FIGS. 120-124. *Androlaelaps patersoni* (Zumpt & Till). Venter (Fig. 120), dorsum (Fig. 121) and chelicera (Fig. 122) of female. Venter (Fig. 123) and chelicera (Fig. 124) of male.

Chaetotaxy of dorsal shield as in the female, but the setae are relatively longer. $DL=569-586\mu$; $DW=324-359\mu$; $DL/DW=1.5$. Holoventral shield reticulate, expanded behind coxae IV and bearing 23 setae. The integument bears about 15 pairs of setae. Chaetotaxy of legs as in the female.

HOST AND LOCALITY: *Gyps coprotheres* (Forster) from Rustenburg, Transvaal (type and other material, S.A.I.M.R.).



FIGS. 125-127. *Androlaelaps phoeniculi* (Zumpt & Till), female. Venter (Fig. 125); dorsum (Fig. 126); chelicera (Fig. 127).

Androlaelaps phoeniculi (Zumpt & Till)

Haemolaelaps phoeniculi Zumpt & Till, 1954; *Rev. Ecuat. Ent. Parasit.* 2 : 209, figs. 1-2.

FEMALE (figs. 125-127): Deutosternum with 6 rows of 1-3 teeth. Chelae 30-32 μ long; pilus dentilis slender; arthrodial filaments subequal in length.

Dorsal shield reticulate, truncate posteriorly, bearing 37 pairs of setae, two pairs being absent from the anterior part of the shield. Lengths of setae *i4* and *z2* do not exceed $\frac{1}{4}$ the distance between their bases; the setae at the anterior end of the shield are longer, *i1* being at least twice as long as *i4*. Posterior terminal seta *Z5* barbed, 5-6 times as long as seta *J5*. $DL=517-579\mu$; $DW=290-340\mu$; $DL/DW=1.6-1.8$.

Sternal shield similar to that of the *mesopicos*-group, but relatively broader. $SL=62-72\mu$; $SW=134-156\mu$; $SL/SW=0.4-0.5$. Anterior and lateral parts of the shield granular and reticulate, remaining part of shield apparently smooth; presternal area reticulate. First pair of sternal setae and metasternal setae subequal in length, second and third pairs slightly longer.

Genital shield extends almost to the anal shield and is apparently without any distinct pattern. It is slightly widened behind the genital setae, with its lateral margins subparallel and its posterior border almost straight. $GW_1=100-114\mu$; $GW_2=88-96\mu$; $GW_1/GW_2=1.0-1.3$. Genital setae as long as first pair of sternal setae, about $1/3$ GW_2 .

Anal shield distinctly longer than broad, anterior margin straight or slightly convex. $AL=93-114\mu$; $AW=72-83\mu$; $AL/AW=1.1-1.4$. Anus situated at less than half its length from the anterior margin of the shield. Postanal seta about $1\frac{1}{2}$ times as long as paranal setae, the latter being level approximately with the middle of the anus.

Integument of idiosoma bears about 29 pairs of ventral and marginal setae; the ventral setae are short, fine and simple, the marginal ones coarser and mostly barbed. Metapodal plates elongate, slightly curved, length to width about 8 : 1.

Tibia III with 9 setae; anterior seta on coxa I at most $1\frac{1}{4}$ times as long as posterior seta. The leg setae are simple and there are no stout, blunt spurs. Legs short and stumpy; length of tarsus IV about 4 times the width at the base.

MALE (not figured): Length 530μ , width 340μ . Holovenal shield narrow behind coxae IV, with a constriction anterior to the anal region. It bears 15 setae, the first pair lying on the presternal area as in the female. Metapodal plates drop-shaped.

HOST AND LOCALITIES: *Phoeniculus purpureus* Miller from Potchefstroom, Transvaal (type series), from Tsessebe, Bechuanaland, and from Northern Rhodesia (S.A.I.M.R.).

Androlaelaps rhodesiensis (Zumpt & Patterson)

Hypoaspis (*Haemolaelaps*) *rhodesiensis* Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* 14 : 82, fig. 4.

Haemolaelaps rhodesiensis, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 243.

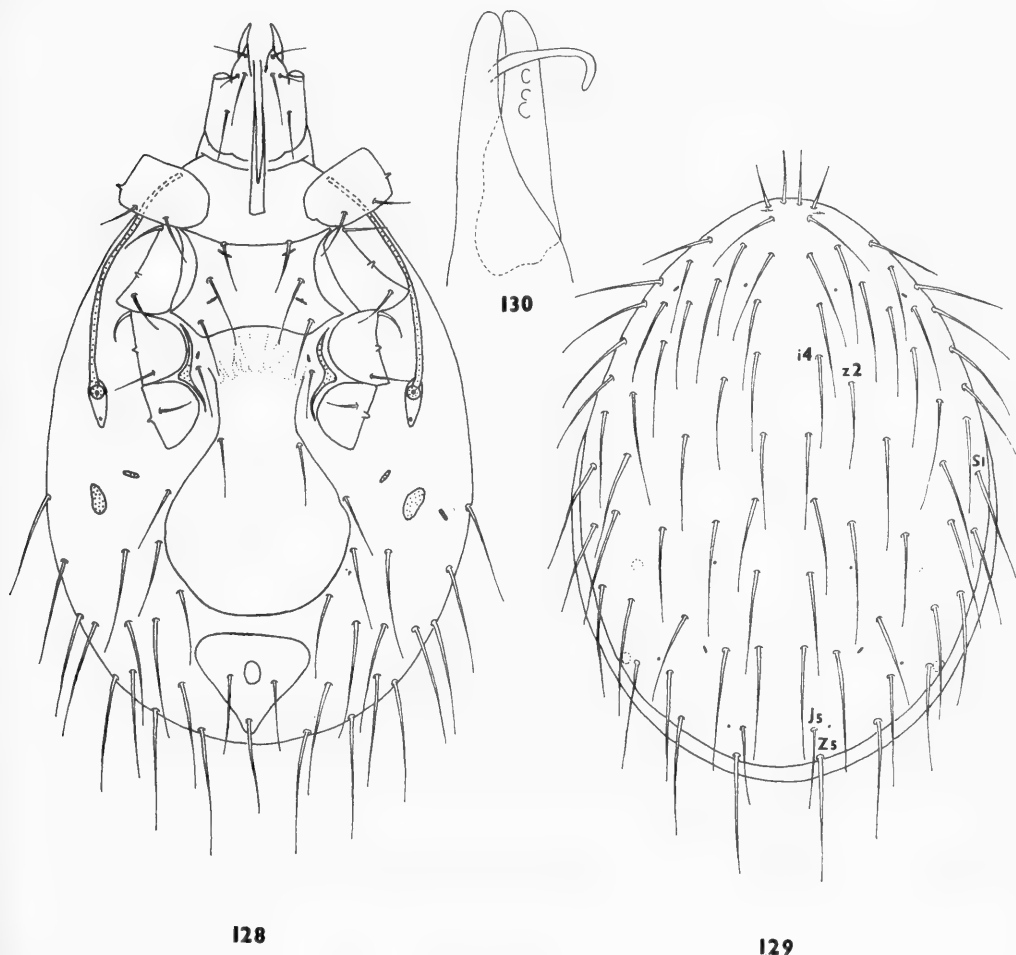
FEMALE (figs. 128-130): Deutosternum provided with 6 rows of 3-5 small teeth. Chelae $62-70\mu$ long; pilus dentilis slightly inflated, ribbon-like; arthrodial filaments subequal in length.

Dorsal shield broadly oval, reticulate, widest about level of seta S_1 . $DL=825-912\mu$; $DW=586-700\mu$; $DL/DW=1.3-1.4$. The shield bears the usual 39 pairs of setae, as well as two accessory setae at the level of J_4 . The setae are all very long, some having fine barbs; lengths of setae i_4 and z_2 exceed twice the distance between their bases; seta J_5 is about $4/5$ as long as seta Z_5 .

Sternal shield reticulate; $SL=114-130\mu$; $SW=170-193\mu$; $SL/SW=0.6-0.7$. Metasternal seta about as long as first sternal seta, second and third sternal setae slightly longer than the first.

Genital shield with a reticulate pattern extending to the anterior flap, greatly expanded behind the fourth pair of coxae. $GW_1=254-300\mu$; $GW_2=130-140\mu$; $GW_1/GW_2=2.0-2.2$. Genital setae relatively short, their length about $2/3$ GW_2 .

Anal shield triangular, broader than long. $AL=150-160\mu$; $AW=170-184\mu$; $AL/AW=0.8-0.9$. Anus slightly more than its length from the anterior margin. Paranal setae inserted slightly behind middle of anus, $2/3$ to $4/5$ as long as the postanal seta.



FIGS. 128-130. *Androlaelaps rhodesiensis* (Zumpt & Patterson), female. Venter (Fig. 128); dorsum (Fig. 129); chelicera (Fig. 130).

Integument of idiosoma bears 15 pairs of long ventral and marginal setae, of which 3 pairs flank the genital shield; most of the setae have fine barbs. Metapodal plates roughly oval, length about twice the width.

Tibia I has 14 and tibia III has 9 setae. Anterior seta on coxa I about $4/5$ as

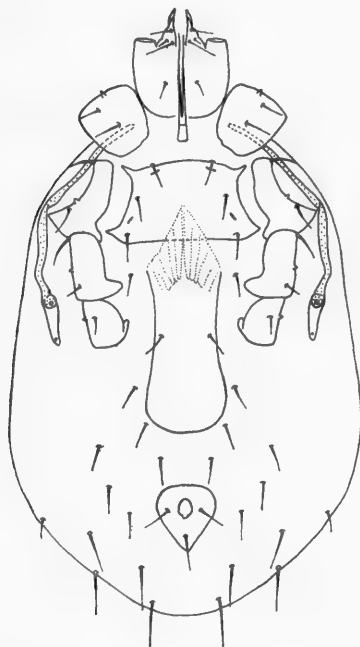
long as posterior seta. Most of the leg setae are barbed; setae on some segments stouter than on others, but there are no blunt spines. Length of tarsus IV about 7 times the width at the base.

MALE: Not known.

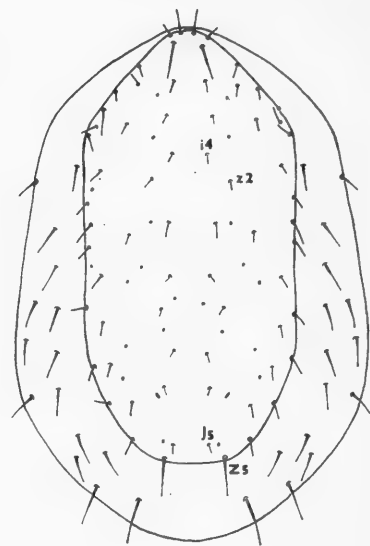
HOSTS AND LOCALITIES: *Saccostomus campestris* Peters from several localities in Southern Rhodesia (S.A.I.M.R.).

Rattus rattus (Linnaeus) and *Rattus morio* (Trouessart) from Brazzaville, French Congo (Zumpt & Till, 1961).

Steatomys pratensis Peters from Southern Rhodesia (one female only, Zumpt & Till, 1961).



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FIGS. 131-132. *Androlaelaps sangsteri* (Radford) female. Venter (Fig. 131); dorsum (Fig. 132).

Androlaelaps sangsteri (Radford)

Liponyssus sangsteri Radford, 1942, *Parasitology* 34 : 190, fig. 11; Zumpt & Till, 1953, *S. Afr. J. Med. Sci.* 18 : 7.

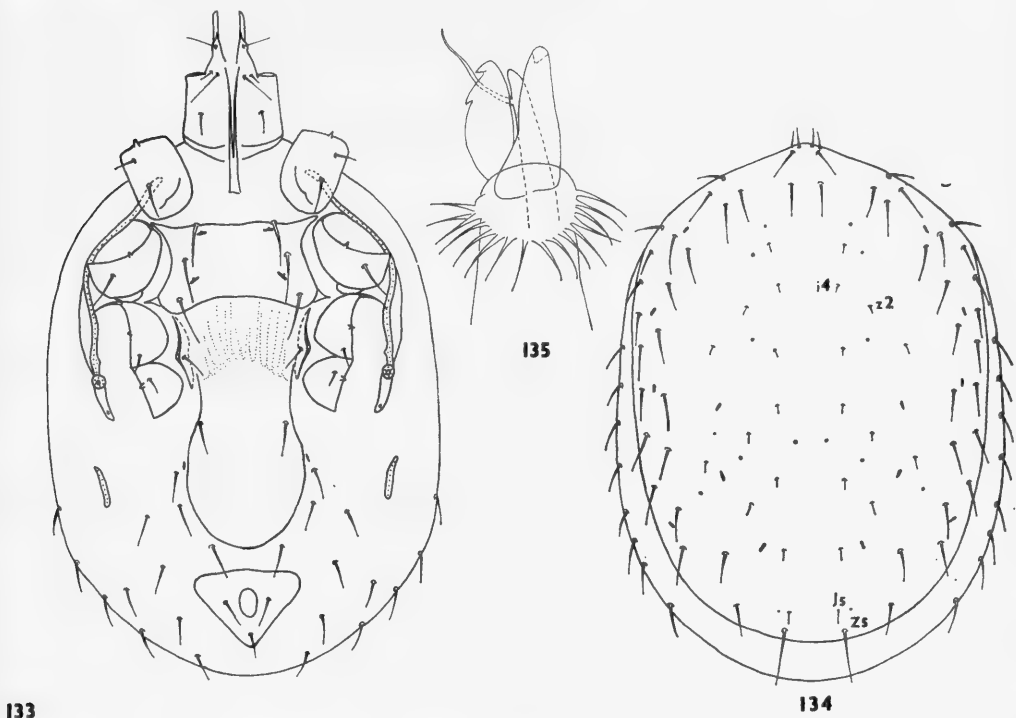
Haemolaelaps sangsteri, Strandtmann & Wharton, 1958, *Manual of Mesostigmatid Mites* : 44.

FEMALE: (figs. 131-132): Deutosternum provided with 6 rows of teeth, 4 teeth in the first row, 2 in the second and one in each of the remaining rows. Corniculi reduced, comparatively small and inconspicuous. Chelicerae missing in the type, the only available specimen.

Dorsal shield narrow with lateral margins subparallel, granular in appearance, with faint reticulations. $DL=518\mu$; $DW=257\mu$; $DL/DW=2.0$. The number of

setae is reduced, only 34 pairs being distinguishable with certainty. Those on the central part of the shield are short, the lengths of setae *i*₄ and *z*₂ not exceeding half the distance between their bases. The anterior and marginal setae are longer; seta *Z*₅ is at least 4 times as long as seta *J*₅ and has fine barbs.

Sternal shield granular, anterior margin slightly convex, posterior margin straight, SL=96 μ ; SW=132 μ ; SL/SW=0.7. Sternal setae subequal in length, relatively short, not reaching bases of following setae. Metasternal setae about as long as sternal setae.



FIGS. 133-135. *Androlaelaps scapularis* (Berlese), female. Venter (Fig. 133); dorsum (Fig. 134); chelicera (Fig. 135).

Genital shield granular, with an indistinct reticulate pattern; widest near its posterior border, between the first and second pairs of flanking setae; anterior part of shield rather sharply pointed. $GW_1=100\mu$; $GW_2=72\mu$; $GW_1/GW_2=1.4$. Length of genital setae about half GW_2 .

Anal shield triangular, approximately as long as broad. AL=82 μ ; AW=79 μ ; Paranal setae level with middle of anus, about 4/5 as long as postanal seta.

Integument of idiosoma bears 26 pairs of ventral and marginal setae, the longer ones near the posterior end of the body being barbed. Metapodal plates not visible.

Legs short and stumpy, their chaetotaxy following the typical *Androlaelaps*

pattern; all the setae simple and hair-like. Length of tarsus IV nearly 4 times the width at the base.

MALE: Not known.

HOST AND LOCALITY: *Protoxerus stangeri* (Waterhouse) from Bwamba Valley, Toro, Uganda (type in B.M.N.H.).

Androlaelaps scapularis (Berlese)

Hypoaspis (*Haemolaelaps*) *scapularis* Berlese, 1918, *Redia* 13 : 124; Keegan, 1956a, *Trans. Amer. micr. Soc.* 75 : 314, figs. 13-14.

Ischnolaelaps bathyergus Radford, 1939, *Parasitology* 31 : 250, figs. 7-8 (*syn. nov.*).

Haemolaelaps eloffi Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 226, figs. 6-9 (*syn. nov.*).

Haemolaelaps natalensis Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 230, figs. 10-11 (*syn. nov.*).

FEMALE (figs. 133-135): Deutosternum provided with 6 rows of 2-4 teeth, the teeth in rows 5 and 6 being very small and inconspicuous; anterior rostral seta at least $1\frac{1}{2}$ times as long as capitular seta. Chelae very small, 18-22 μ long; fixed digit weakly sclerotized, bearing a slender pilus dentilis; movable digit in two parts, one part edentate except for the terminal hook and a small subterminal tooth, the other part dentate but more weakly sclerotized. Arthrodistal filaments subequal in length.

Dorsal shield broadly oval, granular, with a faint reticulate pattern. DL=445-570 μ ; DW=280-390 μ ; DL/DW=1.3-1.6. The shield bears 39 pairs of setae. The centrally situated ones are very small, the lengths of *i*4 and *z*2 being less than 1/5 the distance between their bases; the anterior and marginal setae are longer; seta *Z*5 is at least $2\frac{1}{2}$ times as long as seta *J*5.

Sternal shield granular, presternal area reticulate. SL=41-82 μ ; SW=103-133 μ ; SL/SW=0.4-0.7. Sternal setae subequal in length, first pair slightly shorter than the others; metasternal setae about half as long as third pair of sternal setae.

Genital shield flask-shaped, moderately widened behind the genital setae, granular in appearance, with a faint reticulate pattern. GW₁=103-162 μ ; GW₂=75-105 μ ; GW₁/GW₂=1.2-1.5. Genital setae relatively short, not more than half GW₂.

Anal shield triangular, distinctly wider than long. AL=52-94 μ ; AW=83-114 μ ; AL/AW=0.5-0.7. Paranal setae level approximately with middle of anus, or slightly anterior, about $1\frac{1}{4}$ times as long as postanal seta.

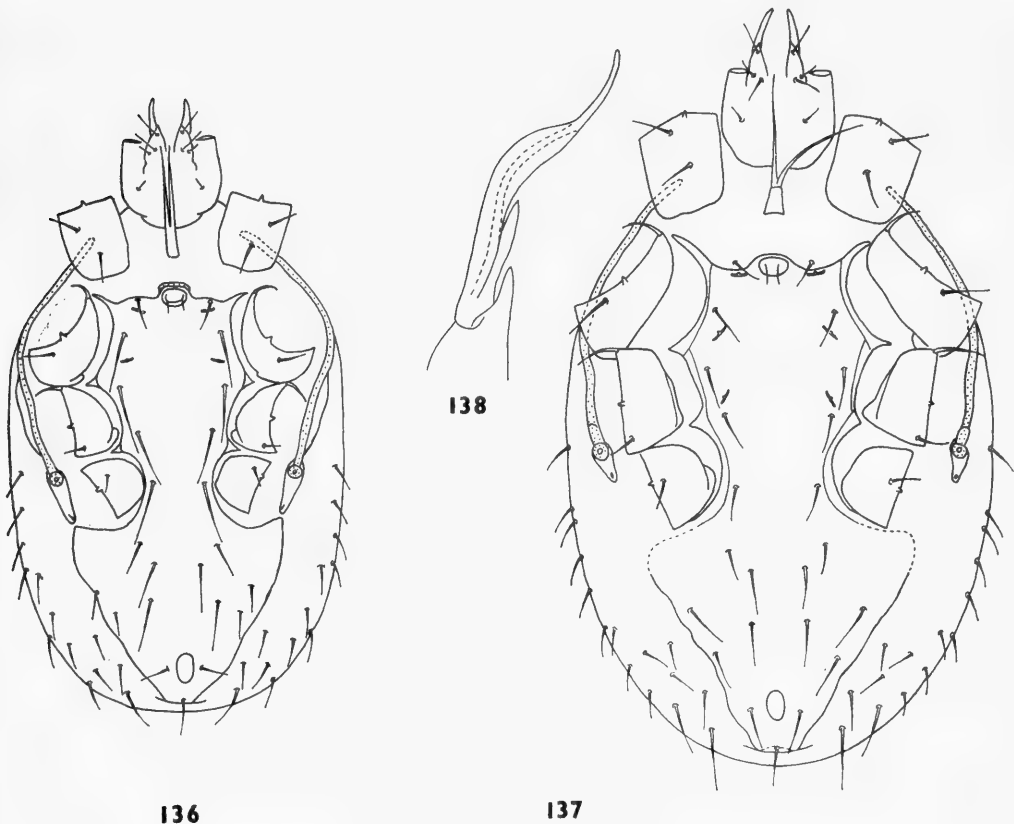
Integument of idiosoma bears about 20 pairs of simple ventral and marginal setae, of which 3 pairs border the genital shield. Metapodal plates elongate, length to width about 6 : 1.

Chaetotaxy of legs normal. Posterior seta on coxa I is $1\frac{1}{4}$ - $1\frac{1}{2}$ times as long as the anterior seta. Anterior seta on coxa III about twice as long and thick as posterior seta. Length of tarsus IV about 4 times the width at the base.

MALE (fig. 136): Fixed digit of chelicera with a slender pilus dentilis as in the female. Dorsal shield as in the female except that the centrally situated setae are relatively longer. Holoventral shield expanded behind coxae IV, bearing 23 setae, 5 pairs lying in the region between coxae IV and the anus. Integument of iosoma with about 13 pairs of setae. Chaetotaxy of legs as in female.

HOSTS AND LOCALITIES: *Bathyergus suillus* (Schreber) from Strandtfontein, Cape Town (types in Dr. C. D. Radford's collection and in M.R.A.C.), and from Tulbagh District, Western Cape Province (S.A.I.M.R.).

Cryptomys hottentotus (Lesson) from Bloemfontein, Orange Free State, and Pietermaritzburg, Natal (S.A.I.M.R. and B.M.N.H.).



FIGS. 136-138. *Androlaelaps scapularis* (Berlese), venter of male (Fig. 136).

Androlaelaps spatuliformis (Lavoipierre), venter (Fig. 137) and chelicera (Fig. 138) of male.

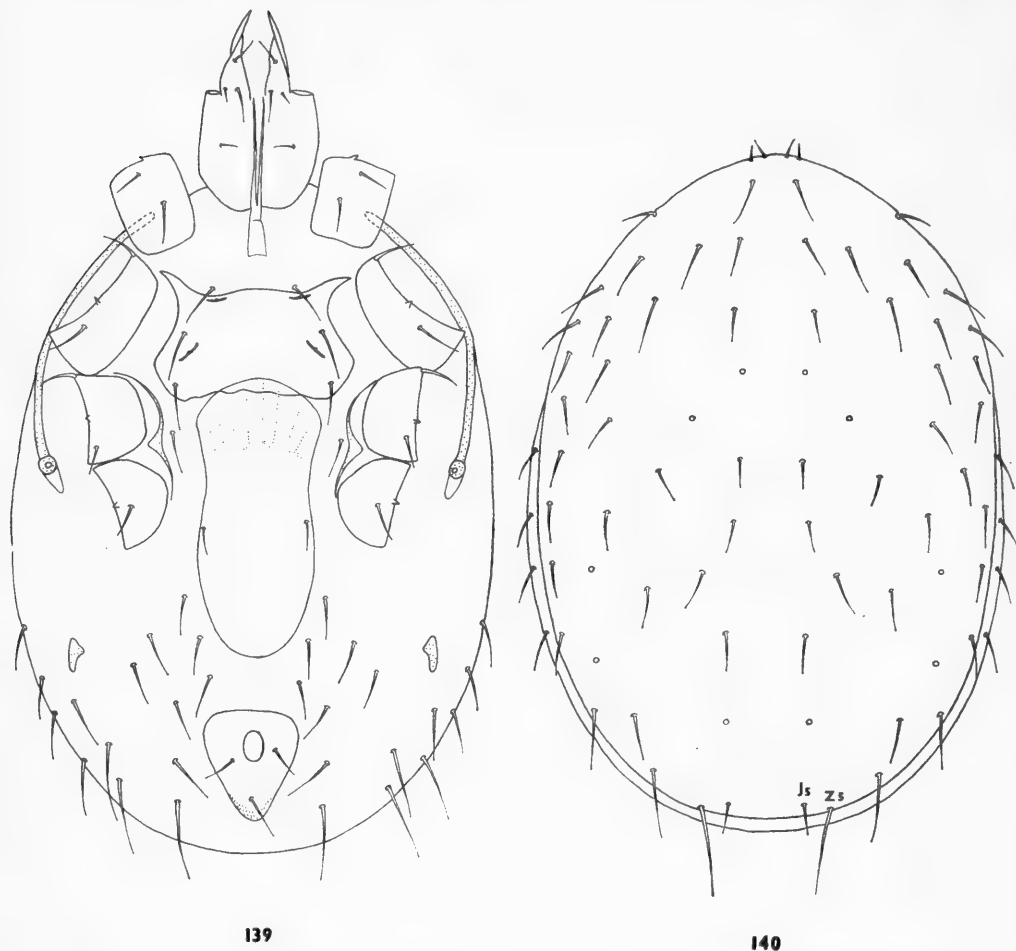
Cryptomys holosericeus (Wagner) from Pietermaritzburg, Natal (S.A.I.M.R.).

NOTE: The specimens from *Bathyergus suillus* are larger than those from the *Cryptomys* species, but there are no reliable features which could be used to separate these groups. The types of *I. bathyergus*, *H. eloffi* and *H. natalensis* have been compared with drawings of the type of *H. scapularis* Berlese made by Dr. F. Gorirossi (Keegan, 1956) and it is believed that they are all conspecific. The deep posterior concavity of the sternal shield, indicated by Zumpt & Till (1953) in their drawing of *H. eloffi*, appears to be the result of over-clearing.

Androlaelaps spatuliformis (Lavoipierre)

Haemolaelaps spatuliformis Lavoipierre, 1956, *Ann. trop. Med. Parasit.* 50 : 293, fig. 2.

FEMALE (figs. 139-140): Deutosternum provided with at least 4 rows of 2-3 small teeth, 5th and 6th rows very indistinct. Chelae about 40μ long; pilus dentilis and arthrodial filaments not clearly visible in the one specimen available for examination.



FIGS. 139-140. *Androlaelaps spatuliformis* (Lavoipierre), female. Venter (Fig. 139); dorsum (Fig. 140).

Dorsal shield oval; $DL=525\mu$; $DW=360\mu$; $DL/DW=1.4$. Several of the setae are missing from the specimen examined, but the chaetotaxy appears to follow the 38- or 39-pair pattern. Seta $\phi x3$ cannot be distinguished in this specimen. Seta $Z5$ is more than twice as long as seta $J5$.

Sternal shield has a few very indistinct reticulations; presternal area weakly

reticulate. Sternal and metasternal setae subequal in length; first pair of sternal setae inserted on presternal area. $SL=94-96\mu$; $SW=140-143\mu$; $SL/SW=0.7$.

Genital shield spatulate in shape, very slightly widened behind genital setae, then tapering gradually; $GW_1=100\mu$; $GW_2=97\mu$. Genital setae relatively short, about $\frac{1}{4} GW_2$.

Anal shield slightly longer than broad; $AL=100-112\mu$; $AW=91\mu$. Paranal setae inserted near posterior margin of anus, about $\frac{3}{4}$ as long as postanal seta.

Integument of idiosoma bears about 19 pairs of ventral and marginal setae. Metapodal plates provided with a pronounced medial protrusion.

Chaetotaxy of legs normal except for genu IV which has only 9 instead of 10 setae. Posterior seta on coxa I about $1\frac{1}{4}$ times as long as anterior seta.

MALE (figs. 137-138): Structure of chelicera indicated in fig. 138; pilus dentilis not visible. Dorsal shield as in female; seta p_{x3} present. $DL=404-409\mu$; $DW=266\mu$; $DL/DW=1.5$. Holoventral shield expanded behind coxae IV, bearing 21 setae, excluding the first pair of sternal setae which is situated on the presternal area. Chaetotaxy of legs as in the female. Anterior and posterior setae of coxae I approximately equal in length and thickness. Femur II has one stout ventral spine and tarsus II has two stout ventral spines.

HOST AND LOCALITY: *Anomaluris derbianus* Gray from Kumba, British Cameroons. One female paratype received on loan from Dr. M. M. J. Lavoipierre, and two males from the type host and locality received from the Liverpool School of Tropical Medicine, by courtesy of Miss M. Johnson.

Androlaelaps spreo (Zumpt & Till)

Haemolaelaps spreo Zumpt & Till, 1956, *Z. Parasitenk.* 17: 290, fig. 9.

FEMALE (figs. 141-143): *Androlaelaps spreo* is very closely allied to *A. dasymys*, differing from it mainly in the structure of the chelicerae. The pilus dentilis is different in shape and the arthrodial filaments are subequal in length. The chelae are $54-56\mu$ long.

The dorsal shield bears 39 pairs of setae as well as 4-6 accessory setae between the *J* series. All the setae are relatively long, the lengths of setae *i4* and *z2* being at least 1.5 times the distance between their bases. The marginal setae are slightly longer and thicker than those on the median part of the shield and are barbed. Seta *Z5* is 1.7-1.8 times as long as seta *J5*. $DL=849-936\mu$; $DW=525-604\mu$; $DL/DW=1.6$.

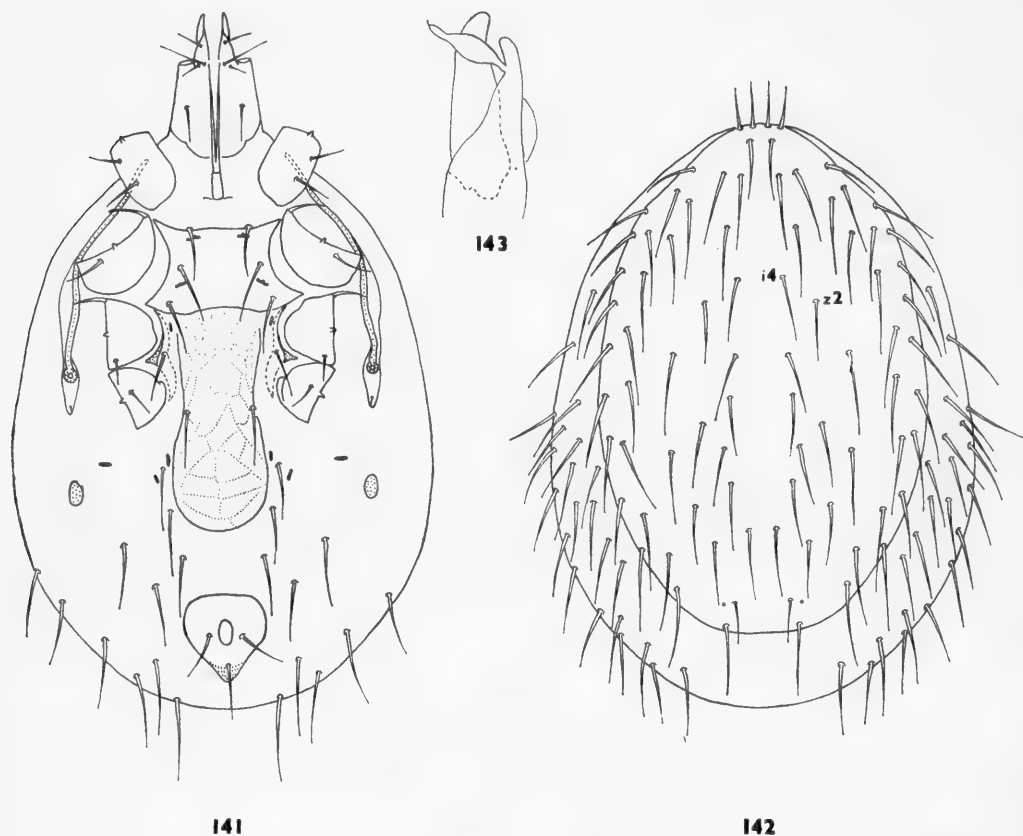
Sternal shield reticulate; $SL=114-140\mu$; $SW=166-175\mu$; $SL/SW=0.7-0.8$. Genital shield slightly widened posteriorly, with a pronounced reticular pattern extending to the anterior margin. $GW_1=158-175\mu$; $GW_2=114-123\mu$; $GW_1/GW_2=1.3-1.4$. Genital setae relatively long, slightly more than $2/3 GW_2$.

Anal shield approximately as long as broad and with a reticular pattern; $AL=140-162\mu$; $AW=140-158\mu$. Anus situated at slightly more than its length from the anterior margin of the shield; paranal setae about $4/5$ as long as postanal seta.

Integument bears about 33 pairs of ventral and marginal setae, the latter being

longer and thicker than the former and provided with barbs. Metapodal plates oval, 1.5–1.8 times as long as broad.

Chaetotaxy of legs normal. Posterior seta on coxa I slightly longer and thicker than anterior seta. Tarsus II has three stout ventral bristles but no blunt spines. Trochanter IV has a stout dorsal bristle. Length of tarsus IV $6\frac{1}{2}$ – $7\frac{1}{2}$ times width at base.



FIGS. 141–143. *Androlaelaps spreco* (Zumpt & Till), female. Venter (Fig. 141); dorsum (Fig. 142); chelicera (Fig. 143).

MALE (figs. 144–145): Chelae as illustrated, pilus dentilis resembling that of female. Dorsal shield bears 8 accessory setae, otherwise chaetotaxy as in female. DL = 675μ ; DW = 447μ ; DL/DW = 1.5. Holoventral shield reticulate, expanded, bearing 23 setae. Chaetotaxy of legs as in female.

HOSTS AND LOCALITIES: *Spreo bicolor* (Gmelin), Springs, Transvaal (type series, S.A.I.M.R.).

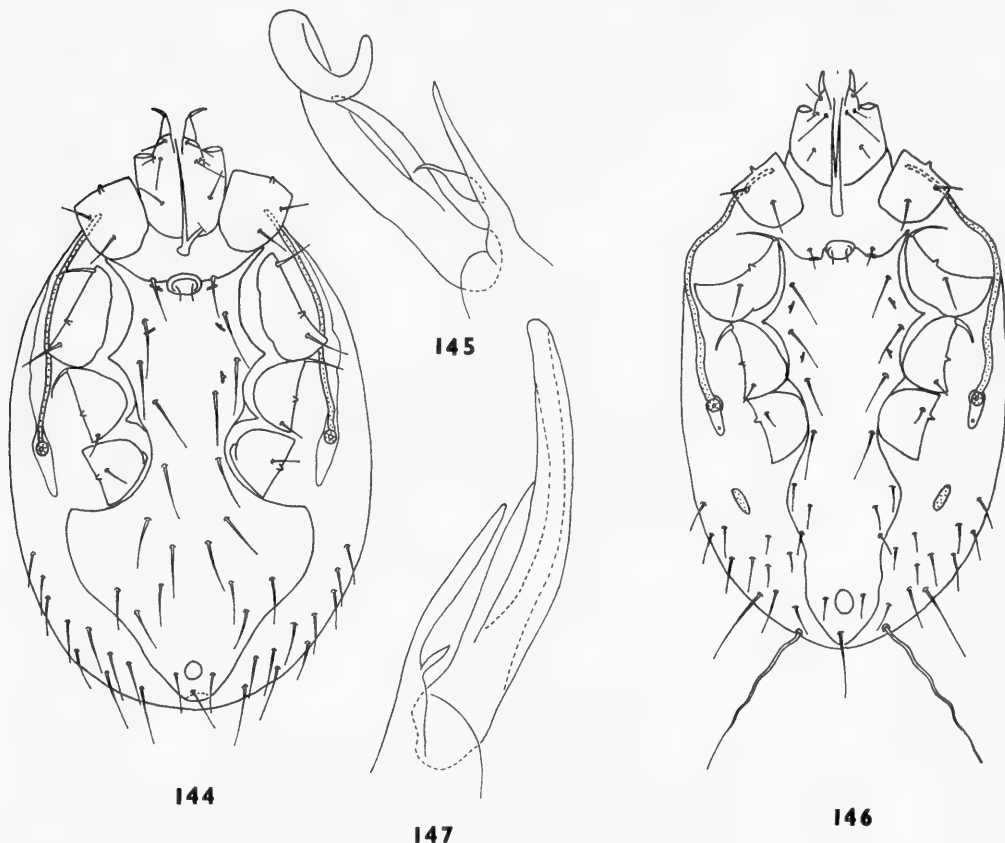
Riparia paludicola (Vieillot), Johannesburg, Transvaal (S.A.I.M.R.).

Androlaelaps steyni (Till)

Haemolaelaps steyni Till, 1959, *J. ent. Soc. S. Afr.* 22 : 430, figs.

FEMALE (figs. 148–150) : This species is very closely allied to *A. mesopicos*. Dorsal shield relatively shorter and broader than in *A. mesopicos* and bearing 38 pairs of setae. $DL=578-648\mu$; $DW=368-420\mu$; $DL/DW=1.5-1.6$.

Sternal shield relatively shorter than in *A. mesopicos*. $SL=53-79\mu$; $SW=$



FIGS. 144–147. *Androlaelaps spreo* (Zumpt & Till), venter (Fig. 144) and chelicera (Fig. 145) of male.

Androlaelaps steyni (Till), venter (Fig. 146) and chelicera (Fig. 147) of male.

$149-166\mu$; $SL/SW=0.3-0.5$. Genital shield similar to that of *A. mesopicos*. Anal shield triangular, with a straight anterior margin; $AL=96-105\mu$; $AW=105-114\mu$; $AL/AW=0.9-1.0$. Postanal seta more than twice as long as paranal setae.

Coxa III has a greatly thickened anterior spine; tarsus IV has only one stout terminal spine. Length of tarsus IV about 5 times width at base.

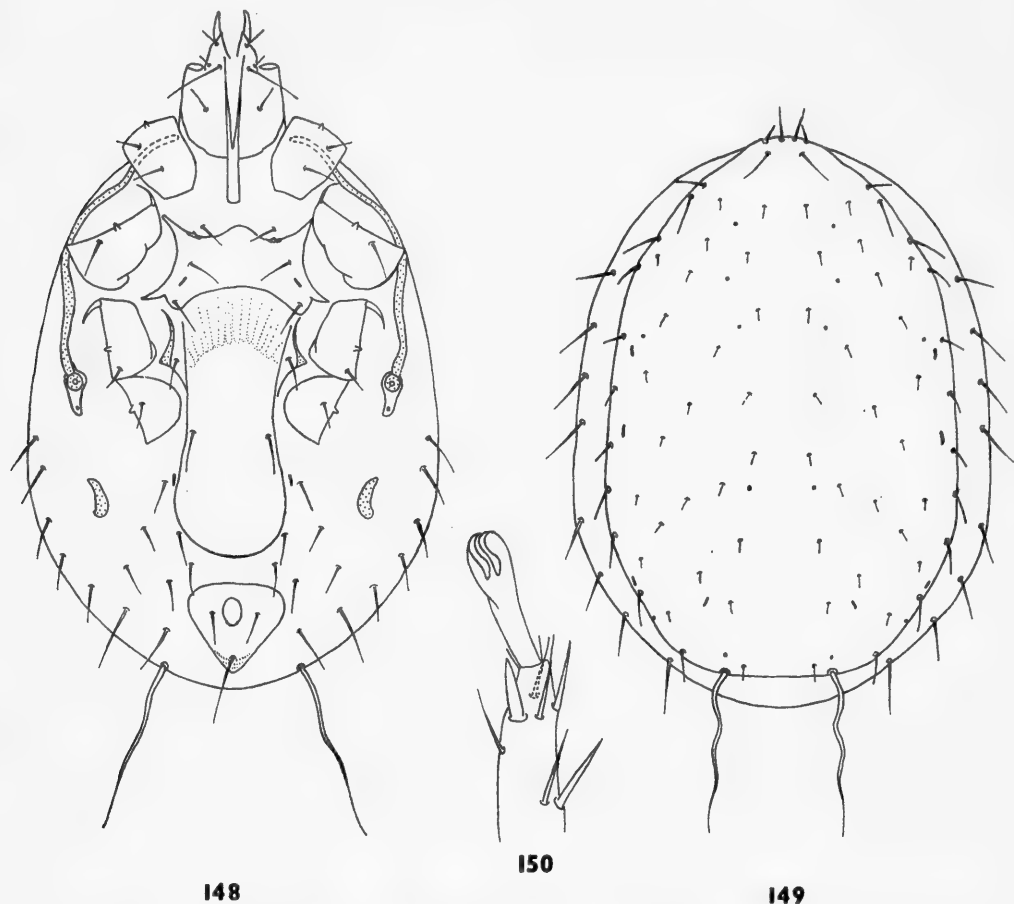
MALE (figs. 146–147) : Chelicera as figured, fixed digit bearing a relatively short, moderately inflated pilus dentilis. Dorsal shield similar to that of female, but

with longer marginal setae. $DL=530-534\mu$; $DW=315-333\mu$; $DL/DW=1.6-1.7$. Coxa III has a stout anterior spine as in the female.

HOSTS AND LOCALITIES: *Lybius torquatus* (Dumont), Mabelikwa, Transvaal (type series, S.A.I.M.R. and B.M.N.H.).

Trachyphonus vaillanti Ranzani, near Johannesburg, Transvaal (S.A.I.M.R.).

Lamprotornis nitens (Linnaeus), Rustenburg, Transvaal (S.A.I.M.R.).



FIGS. 148-150. *Androlaelaps steyni* (Till), female. Venter (Fig. 148); dorsum (Fig. 149); ventral view of tip of tarsus IV (Fig. 150).

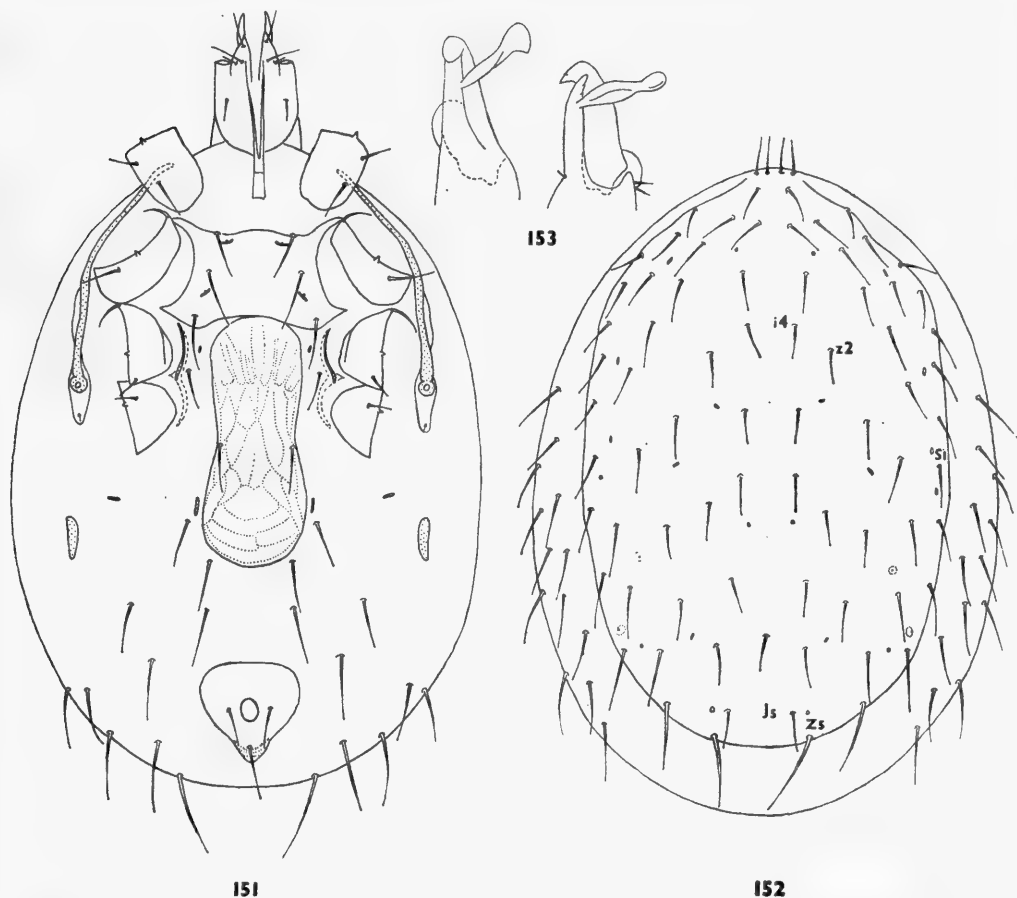
***Androlaelaps suncus* sp. nov.**

FEMALE (figs. 151-153): Deutosternum provided with 6 rows of 2-5 teeth. Chelae about 30μ long; movable digit with a pronounced terminal hook which arches over the tip of the fixed digit; pilus dentilis inflated, hour-glass-shaped in some positions; arthrodial filaments subequal in length.

Dorsal shield oval, reticulate, widest about the level of seta SI . $DL=608-694\mu$;

DW=385-456 μ ; DL/DW=1.5-1.7. The shield bears the usual 39 pairs of setae and one accessory seta. Lengths of setae *i*₄ and *z*₂ about 2/3 the distance between their bases; seta *Z*₅ nearly twice as long as seta *J*₅. Setae *Z*₅ and *S*₃-*S*₅ are barbed, the others appear to be simple.

Sternal shield reticulate, except in the postero-median third. SL = 90-105 μ ;



FIGS. 151-153. *Androlaelaps suncus* sp. nov., female. Venter (Fig. 151); dorsum (Fig. 152); chelicera (Fig. 153).

SW=128-148 μ ; SL/SW=0.7. Metasternal setae and first pair of sternal setae subequal in length, 2nd and 3rd pairs of sternal setae slightly longer.

Genital shield slightly widened behind the genital setae, broadly rounded posteriorly, with a fairly well-marked, overall, reticular pattern. GW₁=105-120 μ ; GW₂=84-103 μ ; GW₁/GW₂=1.2. Length of genital setae about 3/5 GW₂.

Anal shield approximately as long as broad; AL=103-120 μ ; AW=106-115 μ . Anus slightly more than its length from the anterior margin. Paranal setae level approximately with middle of anus, about 5/6 as long as postanal seta.

Integument of idiosoma bears about 23 pairs of ventral and marginal setae, the latter being barbed. Metapodal plates elongate, length to width about 4 : 1.

Chaetotaxy of legs normal. Posterior seta on coxa I is $1\frac{1}{4}$ times as long as anterior seta. Length of tarsus IV about 5 times its width at the base.

MALE: Not known.

HOSTS AND LOCALITIES: *Suncus varius* (Smuts) from Tibedi, Basutoland, 9 October, 1953 (4 females).

Crocidura sp. from Pilgrim's Rest, Transvaal, 14 July 1951 (one female not included in the type series).

Holotype and one female paratype in the collection of the South African Institute for Medical Research, two female paratypes (1962.6.12.18-19) in the collection of the British Museum (Natural History).

Androlaelaps tachyoryctes (Radford)

Haemolaelaps tachyoryctes Radford, 1941, *Parasitology* 33 : 309, figs. 3-4; Keegan, 1956, *J. Egypt. publ. Hlth. Ass.* 31 : 236, figs. 19-21.

Hypoaspis (*Haemolaelaps*) *tachyoryctes*, Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* 14 : 71.

FEMALE (figs. 154-157): Deutosternum provided with 6 rows of 2-4 very small teeth. Chelae 34-36 μ long; pilus dentilis moderately inflated, elongate, tapering to a point; arthrodial filaments subequal in length.

Dorsal shield granular, with a faint reticulate pattern. DL=580-627 μ ; DW=333-350 μ ; DL/DW=1.7-1.8. The shield bears 39 pairs of setae in the type specimens, but in the other material examined several of the *r* series are sometimes off the plate. Most of the setae are relatively short and fine; setae *i*₄ and *z*₂ about half as long as the distance between their bases; seta *Z*₅ at least twice as long as seta *J*₅ and considerably thicker.

Sternal shield granular, presternal area reticulate; SL=70-79 μ ; SW=145-148 μ ; SL/SW=0.5-0.6. First pair of sternal setae situated on presternal area, as long as metasternal setae, 2nd and 3rd pairs of sternal setae longer.

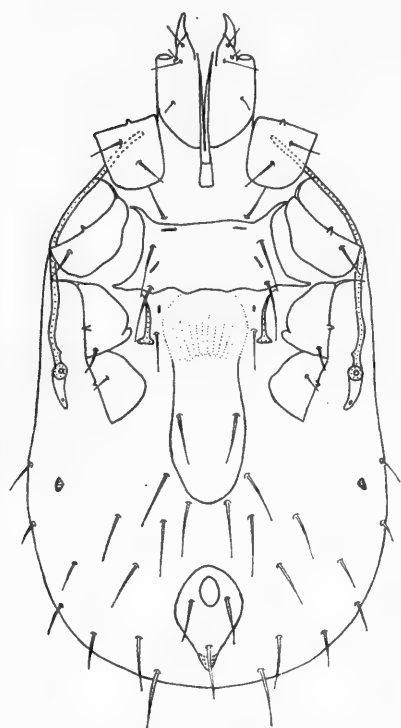
Genital shield granular, slender, tapering behind the genital setae; the length of the latter about $\frac{3}{4}$ GW₂. GW₁=76-86 μ ; GW₂=80 μ .

Anal shield granular, very strongly convex anteriorly. AL=114-122 μ ; AW=72-80 μ ; AL/AW=1.4-1.6. Anus situated at $\frac{1}{3}$ of its length from the anterior margin. Paranal setae level approximately with middle of anus, about $\frac{4}{5}$ as long as postanal seta and thinner.

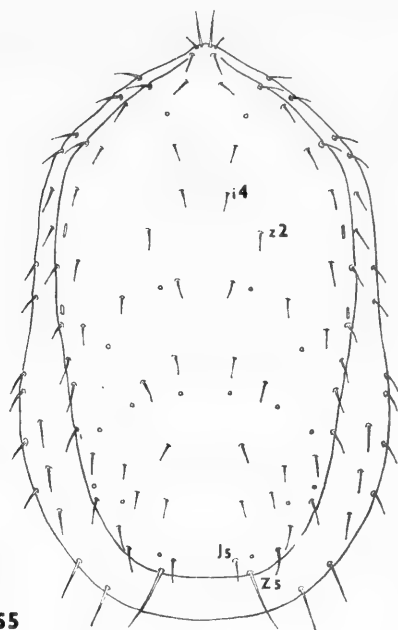
Integument of idiosoma bears 23 pairs of ventral and marginal setae, two pairs of ventral setae bordering the genital shield. Metapodal plates small, nearly triangular in shape, length to width about 2 : 1.

Chaetotaxy of legs normal. Setae on coxa I subequal in length. Tarsus II bears 3 stout ventral setae and 3 stout, blunt, apical setae. Tarsus III has 3, and tarsus IV has 4 stout, rather blunt, apical setae. Length of tarsus IV slightly less than 4 times its width at the base.

MALE (figs. 158-159): Fixed digit of chelicera bears a slightly inflated, tapering pilus dentilis. Chaetotaxy of dorsal shield as in the female, but all the setae are

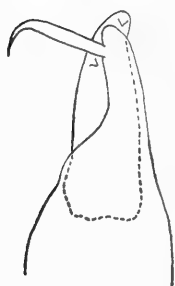


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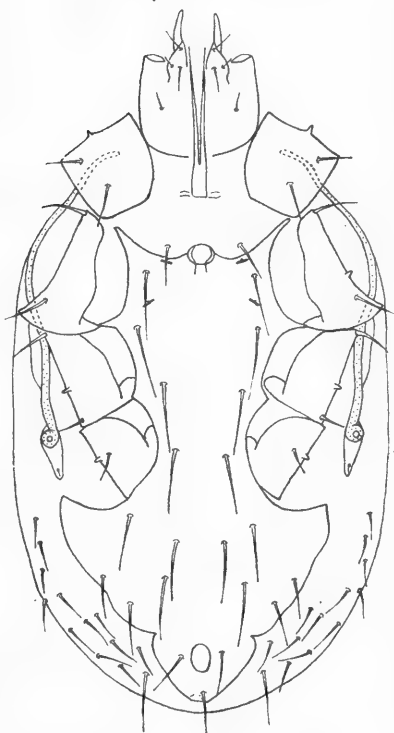
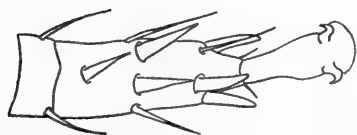
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FIGS. 154-159. *Androlaelaps tachyoryctes* (Radford). Venter (Fig. 154), dorsum (Fig. 155) and chelicera (Fig. 156) of female; ventral view of tarsus II of female (Fig. 157). Venter (Fig. 158) and chelicera (Fig. 159) of male.

situated on the shield. $DL=475-494\mu$; $DW=290-304\mu$; $DL/DW=1.6-1.7$. Holoventral shield greatly expanded behind 4th pair of coxae and bears 23 setae, 5 pairs in the region between coxae IV and the anus. Integument of idiosoma bears 13 pairs of setae. Chaetotaxy of legs as in female.

HOSTS AND LOCALITIES: *Tachyoryctes splendens* (Rüppell) from several localities in Kenya (types in B.M.N.H., other material presented by Miss J. B. Walker to S.A.I.M.R.).

Lemniscomys striatus (Linnaeus), Njoro, Rift Valley Province, Kenya (Keegan, 1956).

Androlaelaps taterae (Zumpt & Patterson)

Hypoaspis (*Haemolaelaps*) *taterae* Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* 14 : 83, fig. 6.
Haemolaelaps taterae, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 244.

FEMALE (figs. 160-162): *A. taterae* is very closely allied to *A. villosissimus*, differing from it chiefly in being more densely haired. This is particularly noticeable in the region between the genital and anal shields, where there are about 13 setae, and in the area between the genital shield and the metapodal plates.

The chelae of *A. taterae* are $44-48\mu$ long; pilus dentilis strongly inflated basally, terminal half slender and sharply bent; arthrodial filaments variable in size, the longest being about twice the average length.

Dorsal shield faintly reticulate and has a dense overall covering of setae. $DL=813-900\mu$; $DW=480-550\mu$; $DL/DW=1.6-1.7$.

Sternal shield reticulate, sharply demarcated from the reticulate and granular presternal area. $SL=128-148\mu$; $SW=166-175\mu$; $SL/SW=0.8-0.9$. Metasternal setae nearly as long as first pair of sternal setae; the latter are barbed.

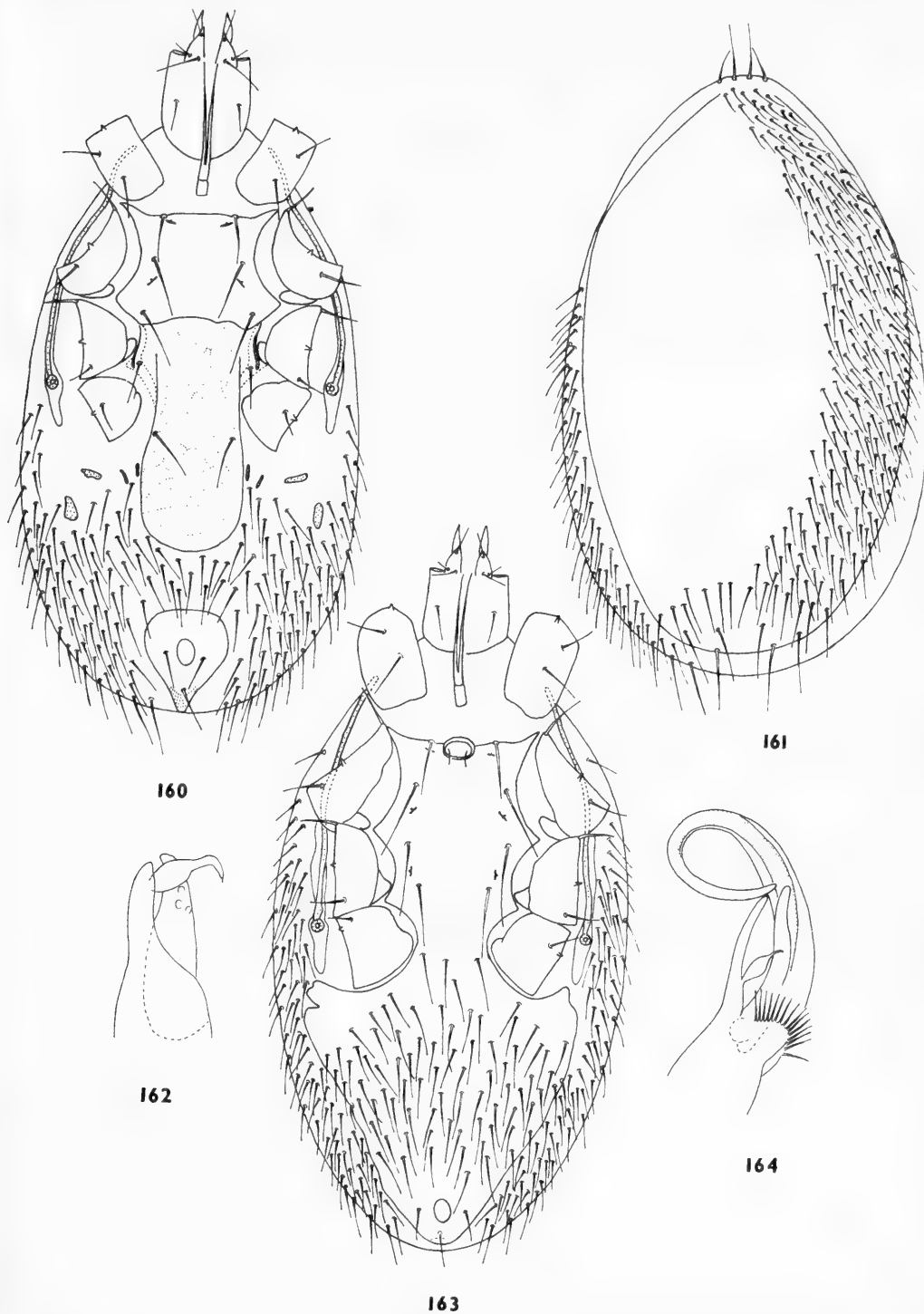
Genital shield with an overall reticular and granular pattern, slightly widened posteriorly. $GW_1=150-162\mu$; $GW_2=135-140\mu$; $GW_1/GW_2=1.1-1.2$. Length of genital setae about $3/5 GW_2$.

Anal shield reticulate; $AL=152-162\mu$; $AW=124-138\mu$; $AL/AW=1.1-1.2$. Anus situated at approximately its length from the anterior margin. Paranal setae level with middle of anus, about $4/5$ as long as postanal seta. Metapodal plates roughly oval, length about $1\frac{1}{2}-2\frac{1}{2}$ times the width.

Genu III bears 10 setae, tibia III bears 9, otherwise the chaetotaxy of the legs follows the normal pattern for the genus. Posterior seta on coxa I slightly longer than anterior seta; many leg setae barbed. Length of tarsus IV is 9 times its width at the base.

MALE (figs. 163-164): Chelicera as figured, the fixed digit bearing a pilus dentilis similar to that of the female. Dorsal shield and integument as in female; $DL=599\mu$; $DW=359\mu$; $DL/DW=1.7$. Holoventral shield reticulate, bearing numerous setae on the posterior portion.

HOSTS AND LOCALITIES: Widely distributed in Southern Africa on *Tatera afra* (Gray). Single specimens have been recorded from *Rattus natalensis* (Smith), *Rattus chrysophilus* (de Winton) and *Otomys irroratus* (Brants) (S.A.I.M.R., B.M.N.H., and M.R.A.C.).



FIGS. 160-164. *Androlaelaps taterae* (Zumpt & Patterson). Venter (Fig. 160), dorsum (Fig. 161) and chelicera (Fig. 162) of female. Venter (Fig. 163) and chelicera (Fig. 164) of male.

***Androlaelaps tateronis* (Radford)**

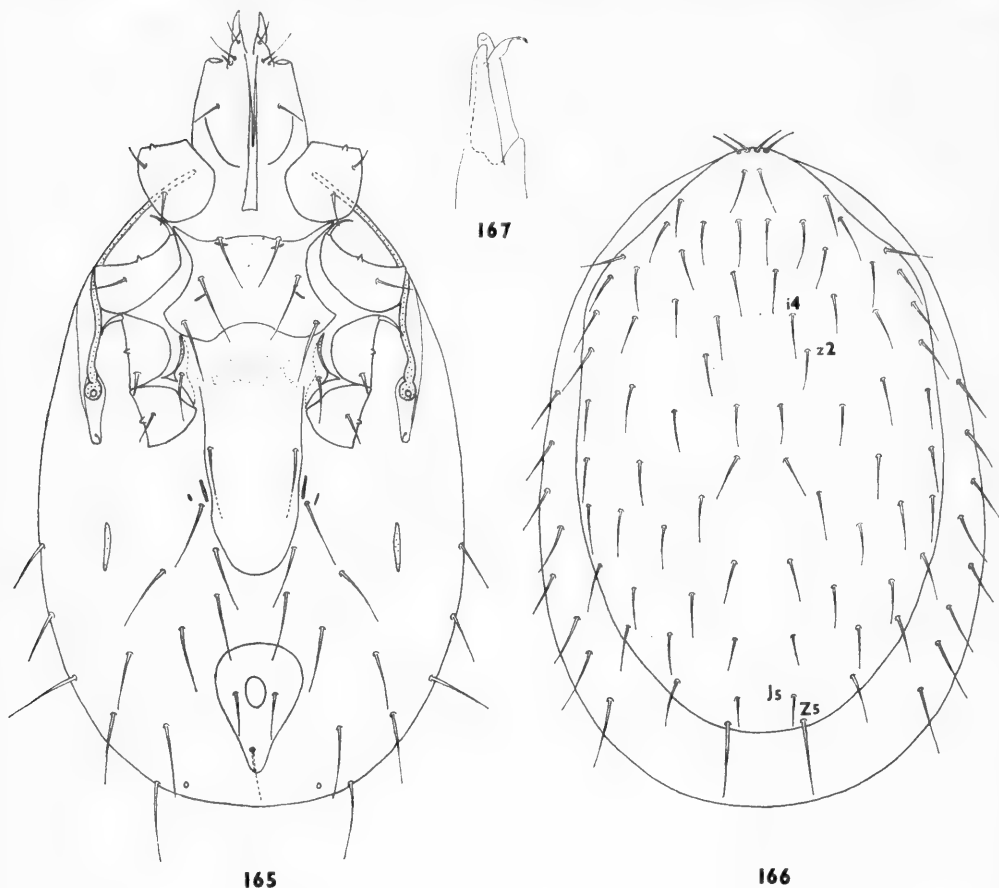
Ischnolaelaps tateronis Radford, 1939, *Parasitology* 31 : 247, fig. 4.

Hypoaspis (*Haemolaelaps*) *tateronis*, Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* 14 : 71.

Haemolaelaps tateronis, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 242.

Haemolaelaps radfordi Keegan, 1956, *J. Egypt. publ. Hlth. Ass.* 31 : 241, figs. 24-25 (*syn. nov.*).

FEMALE (figs. 165-167): Deutosternum provided with 6 rows of 2-4 teeth. Chelae



FIGS. 165-167. *Androlaelaps tateronis* (Radford), female. Venter (Fig. 165); dorsum (Fig. 166); chelicera (Fig. 167).

about 36μ long; pilus dentilis inflated basally, terminal portion slender and curved; arthrodial filaments subequal in length.

Dorsal shield oval, reticulate. $DL=656-664\mu$; $DW=400-409\mu$; $DL/DW=1.6-1.7$. The shield bears 39 pairs of setae of moderate length; lengths of setae *i4* and *z2* approximately equal to the distance between their bases; seta *Z5*, the longest on the shield, is about twice as long as seta *J5*.

Sternal shield reticulate, sharply demarcated from granular and reticulate

presternal area. $SL=101-116\mu$; $SW=136-137\mu$; $SL/SW=0.7-0.9$. Metasternal seta about as long as first sternal seta, second and third setae slightly longer.

Genital shield narrow, tapering behind genital setae, with a reticulate pattern which extends to the anterior margin. $GW_2=106-113\mu$; genital setae extend beyond bases of first pair of flanking setae, their length about $3/4 GW_2$.

Anal shield pear-shaped. $AL=124-139\mu$; $AW=96-106\mu$; $AL/AW=1.3$. Anus situated at about its length from the anterior margin; paranal setae level approximately with middle of anus, about as long as postanal seta.

Integument of idiosoma bears 21 pairs of setae, of which 2 pairs flank the genital shield, a third pair being placed between the genital and anal shields. Some of the longer setae have very fine barbs. Metapodal plates slender, length to width about 6 : 1.

Tibia III has 9 setae; the number on tibia II is not clear in all the specimens examined, but is either 9 or 10. Posterior seta on coxa I twice as long as anterior seta and considerably thicker. Anterior seta on coxa II and both setae on coxa III thickened. Three of the apical setae on tarsus II stout and spine-like, one of them blunt. Length of tarsus IV 6 times the width at the base.

MALE: Not known.

HOSTS AND LOCALITIES: *Tatera valida* (Bocage), Gulu District, Uganda (syntype of *I. tateronis* in B.M.N.H.).

"Rat", Yei, Sudan (paratype of *H. radfordi* in B.M.N.H.).

Tatera nigricauda Peters, Lali Hills, Kenya (S.A.I.M.R.).

Unidentified rodents from Uganda (B.M.N.H.) and from the Cameroons (I.R.S.C.).

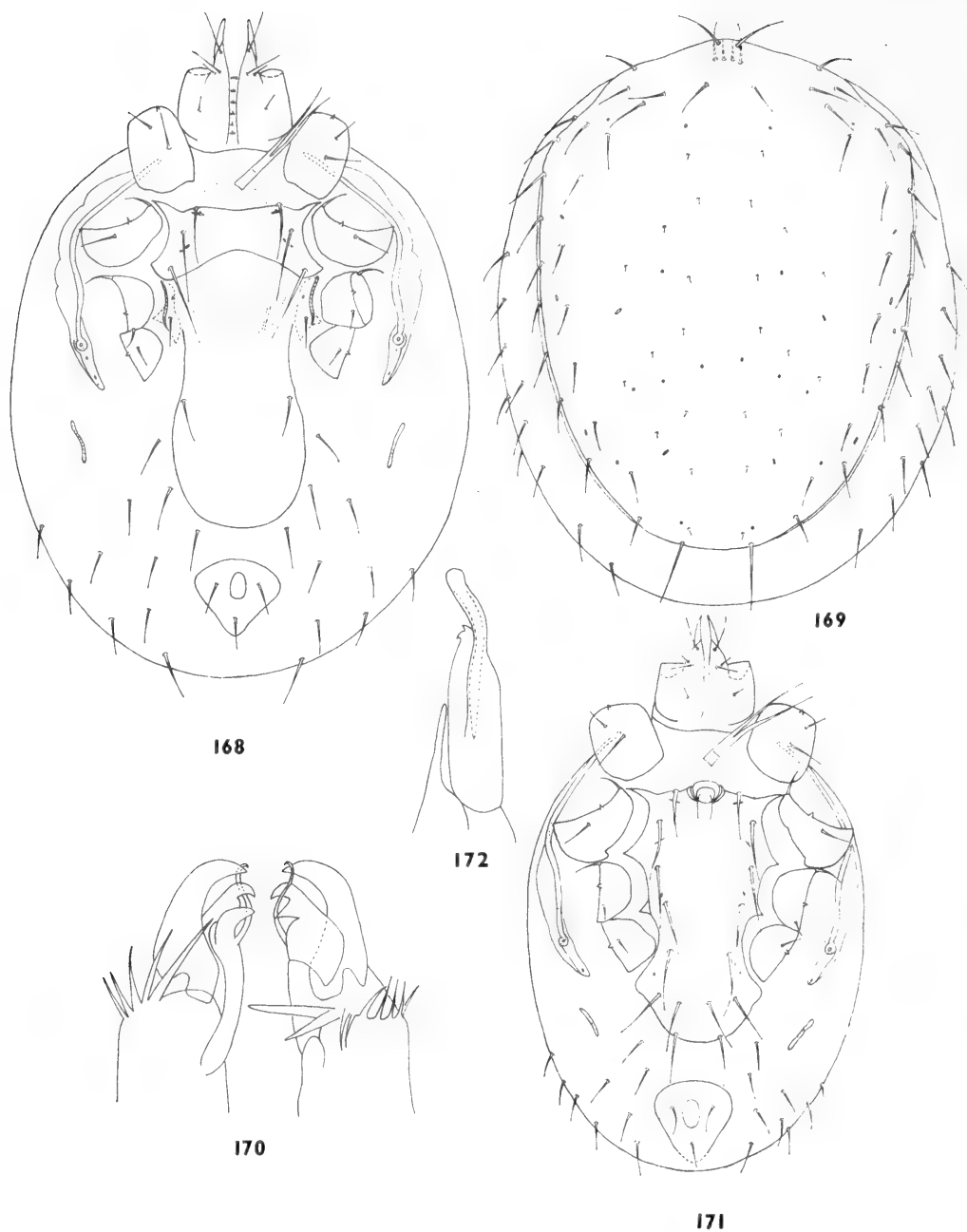
Androlaelaps tauffliebi sp. nov.

FEMALE (figs. 168-170): Deutosternum provided with 6 rows of 3-4 teeth; anterior rostral seta twice as long as capitular seta. Chelae 24μ long; movable digit divided into two parts, a ventral (medial) part which is edentate, except for the terminal hook, and a dorsal (external) part which is broad and dentate. Fixed digit weakly sclerotized, bearing a flagellar pilus dentilis. About 4 of the arthrodial filaments conspicuously long and stout.

Dorsal shield widest about level of seta r_5 , with a granular appearance and very faint indications of a reticular pattern. Laterally it has a distinct double outline. $DL=532-560\mu$; $DW=400-418\mu$; $DL/DW=1.3-1.4$. The shield bears the usual 39 pairs of setae, i_3-i_5 , z_2-z_3 , J_1-J_5 , and px_2-px_3 being reduced to microsetae. Seta Z_5 five times as long as seta J_5 . In all the specimens examined the anterior margin of the shield is tucked under, so that setae s_1 become marginal in position and i_1 and r_1 are ventral.

Sternal shield about 3 times as wide as long, deeply concave posteriorly, granular in appearance. $SL=43-48\mu$; $SW=138-143\mu$; $SL/SW=0.30-0.35$. Sternal seta III nearly $1\frac{1}{2}$ times as long as sternal seta I; metasternal seta short and fine, about half as long as sternal seta I.

Genital shield large, broadly rounded posteriorly, granular. $GW_1=142-157\mu$; $GW_2=120-133\mu$; $GW_1/GW_2=1.2-1.3$. Genital setae short, about $1/3 GW_2$.



FIGS. 168-172. *Androlaelaps tauffiebi* sp. nov. Venter (Fig. 168); dorsum (Fig. 169) and chelicera (Fig. 170) of female. Venter (Fig. 171) and chelicera (Fig. 172) of male.

Anal shield with some granulation and striations laterally. $AL=77-79\mu$; $AW=91-98\mu$; $AL/AW=0.8-0.9$. Anus situated at about half its length from the anterior margin. Paranal setae inserted near anterior third of anus, about the same length as the postanal seta.

Integument of idiosoma bears about 20 pairs of setae, some of the marginal ones having fine barbs. Metapodal plates very long and slender, length about 10 times width.

Chaetotaxy of legs normal, setae simple, without any marked modifications. Posterior seta on coxa I approximately $1\frac{1}{2}$ times as long as anterior seta and slightly thicker. Length of tarsus IV about 6 times its width at the base.

MALE (figs. 171-172): Deutosternum and gnathosomal setae as in female. Chelicera provided with an elongate spermadactyl; minute teeth present at tip of movable digit; fixed digit reduced, membranous. Total length of chela about 55μ .

Dorsal shield as in female. $DL=418\mu$; $DW=295\mu$; $DL/DW=1.4$. Sterni-ventral shield separated from anal shield, granular in appearance, with faint indications of reticulation, and bearing 8 pairs of setae. Anal shield approximately as long as broad, otherwise similar to that of female. Metapodal plates relatively broader than in the female.

Chaetotaxy of legs as in female, except that three setae on leg II are strongly inflated, namely, the upper, antero-ventral seta on femur II, upper antero-ventral seta on tibia II, and postero-ventral seta on tarsus II.

HOST AND LOCALITY: Seven females and one male from *Cryptomys mechowii* Peters, Lac Calundo, Angola, 6 January, 1955 (from the collection of Dr. R. Taufflieb, I.R.S.C., leg. A. de Barros Machado).

Holotype (1962.2.12.20), allotype (1962.6.12.21) and two female paratypes (1962.6.12.22-23) in the collection of the British Museum (Natural History); two female paratypes presented to Dr. R. Taufflieb, Institut de Recherches Scientifiques au Congo; two female paratypes presented to the Dundo Museum, Angola.

Androlaelaps theseus Zumpt

Hypoaspis (Androlaelaps) theseus Zumpt, 1950, *Parasitology* 40 : 301, figs. 3-4.

Turkiella theseus, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 225.

Androlaelaps theseus, Cooreman, 1954, *Ann. Mus. Congo Belge Tervuren, Zool.* 1 : 163, figs. 1-4.

FEMALE (figs. 173-175): Deutosternum provided with 6 rows each of 4-8 teeth. Chelae $106-108\mu$ long; pilus dentilis slender, arthroal filaments subequal.

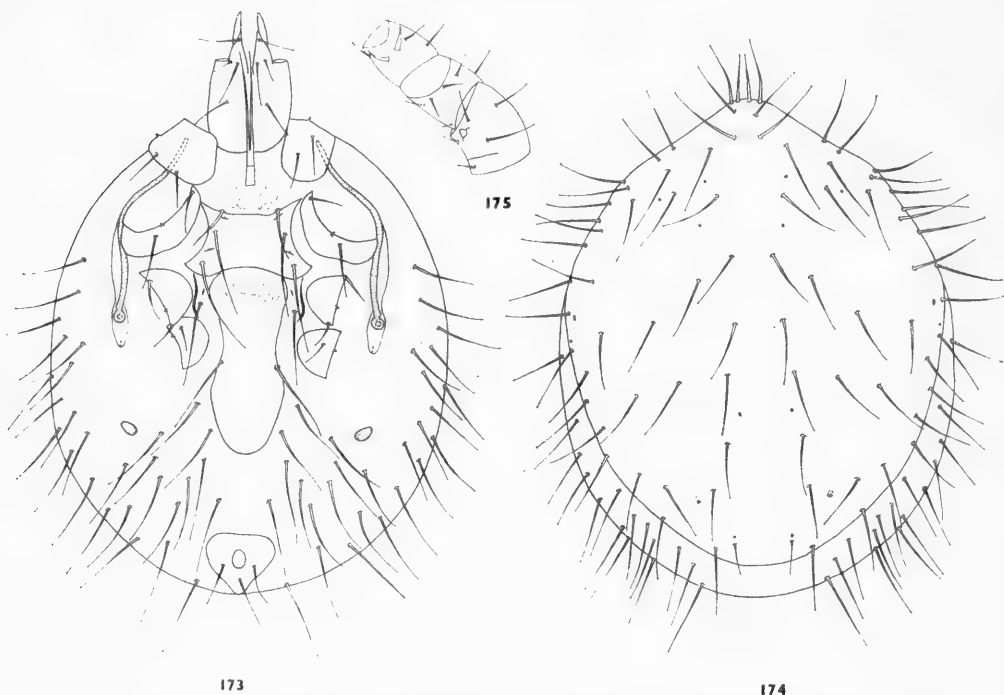
Dorsal shield reticulate and granular. $DL=1350-1570\mu$; $DW=1100-1235\mu$; $DL/DW=1.2-1.3$. The shield bears 40 pairs of setae, an additional pair being present in the *ax* position. The setal lengths vary in mites from different hosts. Seta *r1* distinctly longer than seta *i1*; setae *i4* and *z2* slightly longer than the distance between their bases; seta *Z5* at least $1\frac{1}{2}$ times as long as seta *J5*.

Sternal shield granular and reticular, anterior and posterior margins concave. $SL=143-170\mu$; $SW=266-276\mu$; $SL/SW=0.5-0.6$. First sternal seta reaches almost to base of third; second and third sternal and metasternal setae at least $1\frac{1}{2}$ times as long as first sternal seta.

Genital shield granular, slender, very slightly widened behind genital setae, then tapering posteriorly. $GW_1=205-247\mu$; $GW_2=190-220\mu$; $GW_1/GW_2=1.1-1.2$. Length of genital setae exceeds the width of the shield at the level of their bases.

Anal shield reticulate and granular. $AL=180-205\mu$; $AW=209-238\mu$; $AL/AW=0.8-1.0$. Anus situated at approximately its length from the anterior margin. Paranal setae level with posterior half of anus, about $\frac{3}{4}$ as long as postanal seta.

Integument of idiosoma bears about 42 pairs of ventral and marginal setae, many of which appear to be barbed. Metapodal plates broadly oval, length approximately $1\frac{1}{2}$ times breadth.



FIGS. 173-175. *Androlaelaps theseus* Zumpt, female. Venter (Fig. 173); dorsum (Fig. 174); ventral view of femur, genu and tibia of leg II (Fig. 175).

Chaetotaxy of legs normal. Anterior and posterior setae on coxae I subequal in length, the posterior one slightly thicker. Spur on second femur relatively small, its length being about $1/5$ the width of the femur. Inner and outer ventral setae on tibia II subequal in length and thickness; inner and outer ventral setae on genu II both simple. Tarsus II has 3 stout, blunt, terminal spines. Length of tarsus IV about 7 times its width at the base.

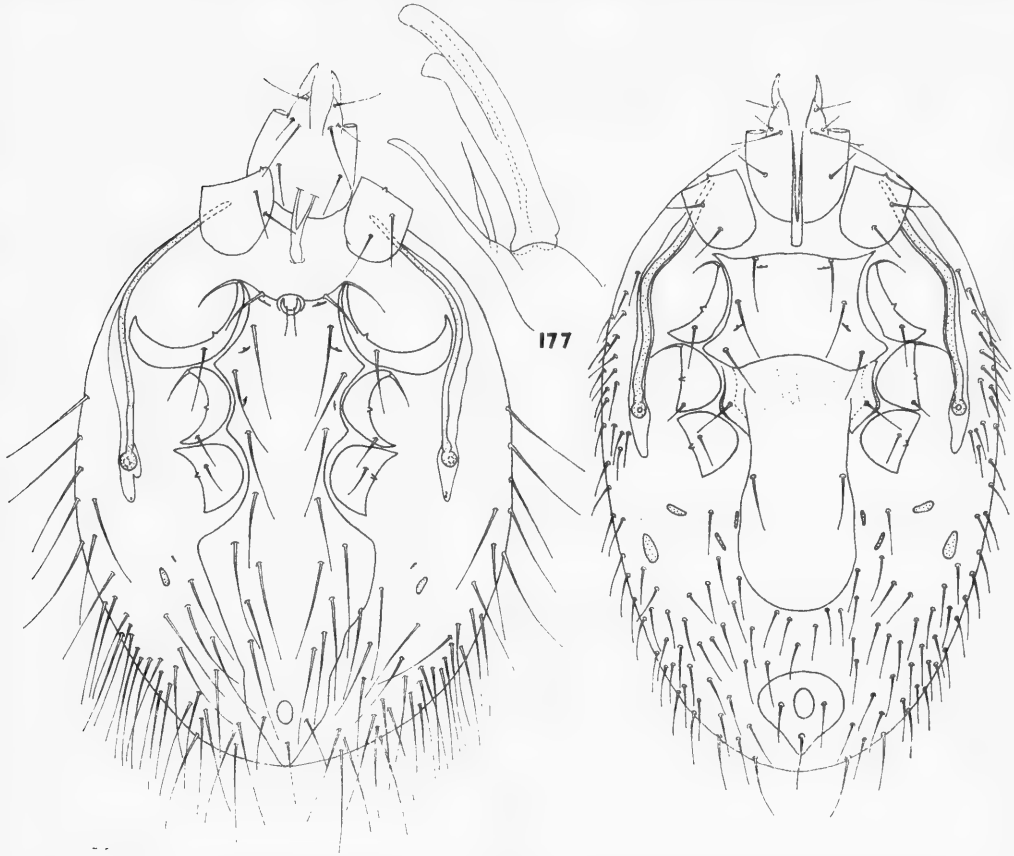
MALE (fig. 176-177): Gnathosoma as in female; fixed digit of chelicera elongate, membranous, bearing a slender pilus dentilis.

Dorsal shield resembles that of female; $DL=1283-1302\mu$; $DW=920-940\mu$; $DL/DW=1.4$. Holoventral shield strongly reticulate and also granular, not

expanded behind coxae IV, bearing 23 setae of which 10 (6+4) are situated in the preanal region behind coxae IV.

Chaetotaxy of legs as in female, but with inner ventral seta on tibia II stouter, and inner ventral seta on genu II shorter and stouter.

HOSTS AND LOCALITIES: Widely distributed in Southern Africa on *Tatera afra* (Gray), and found occasionally on *Rattus natalensis* (Smith), *Rattus chrysophilus*



FIGS. 176-178. *Androlaelaps theseus* Zumpt, venter (Fig. 176) and chelicera (Fig. 177) of male. *Androlaelaps villosissimus* (Berlese), venter female (Fig. 178).

(De Winton), *Acomys cahirinus* (Desmarest), *Saccostomus campestris* Peters and *Steatomys pratensis* Peters (Zumpt & Till, 1961). Recorded from *Tatera afra* (Gray) in the Belgian Congo (Cooreman, 1954). Material in S.A.I.M.R. and B.M.N.H.

***Androlaelaps villosissimus* (Berlese)**

Hypoaspis (*Haemolaelaps*) *villosissimus* Berlese, 1918, *Redia* 13 : 128; Zumpt & Patterson, 1951, *J. ent. Soc. S. Afr.* 14 : 72, fig. 5.

Haemolaelaps villosissimus, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 244; Keegan, 1956a, *Trans. Amer. micr. Soc.* 75 : 314, figs. 1-2.

FEMALE (fig. 178): Deutosternum provided with 6 rows of 3-4 small teeth. Chelae 40μ long; pilus dentilis and arthrodial filaments indistinct.

Dorsal shield with only faint indications of a reticular pattern. $DL=718-744\mu$; $DW=429-455\mu$; $DL/DW=1.6-1.7$. The shield has a dense overall covering of setae which completely obscures any pattern. Most of the setae appear to have fine barbs.

Sternal shield reticulate, sharply demarcated from presternal area. $SL=110-120\mu$; $SW=153-162\mu$; $SL/SW=0.7-0.8$. Metasternal setae as long as first pair of sternal setae.

Genital shield granular, with an overall reticular pattern. $GW_1=140-144\mu$; $GW_2=118-123\mu$; $GW_1/GW_2=1.1-1.2$. Length of genital seta about half GW_2 .

Anal shield reticulate anteriorly and antero-laterally and also granular in appearance. $AL=105-114\mu$; $AW=96-100\mu$; $AL/AW=1.1-1.2$. Anus less than its length from the anterior margin of the shield. Paranal setae level with middle of anus, about $4/5$ as long as postanal seta.

Integument of idiosoma bears numerous setae, 8 or 9 being situated between the genital and anal shields. The ventrally placed setae appear to be simple, whereas the marginal ones are barbed. Metapodal plates oval, length about twice width.

Genu III bears 10 setae and tibia III bears 9; otherwise the chaetotaxy follows the normal *Androlaelaps* pattern. Posterior seta of coxa I slightly longer than anterior seta; many leg setae barbed. Length of tarsus IV 10 times width at base.

MALE: Not known.

HOSTS AND LOCALITIES: *Saccostomus campestris* Peters, Zululand (Berlese, 1918) and Bulawayo, Southern Rhodesia (S.A.I.M.R.). Unidentified rodent from the Cameroons (I.R.S.C.).

Androlaelaps walkerae sp. nov.

FEMALE (figs. 179-181): The hypostomal processes form two pairs of prominent brushes, one ventral in position and the other dorsal. Deutosternum provided with 6 rows of 2-3 teeth. Chelae about 48μ long; pilus dentilis slender; arthrodial filaments subequal in length.

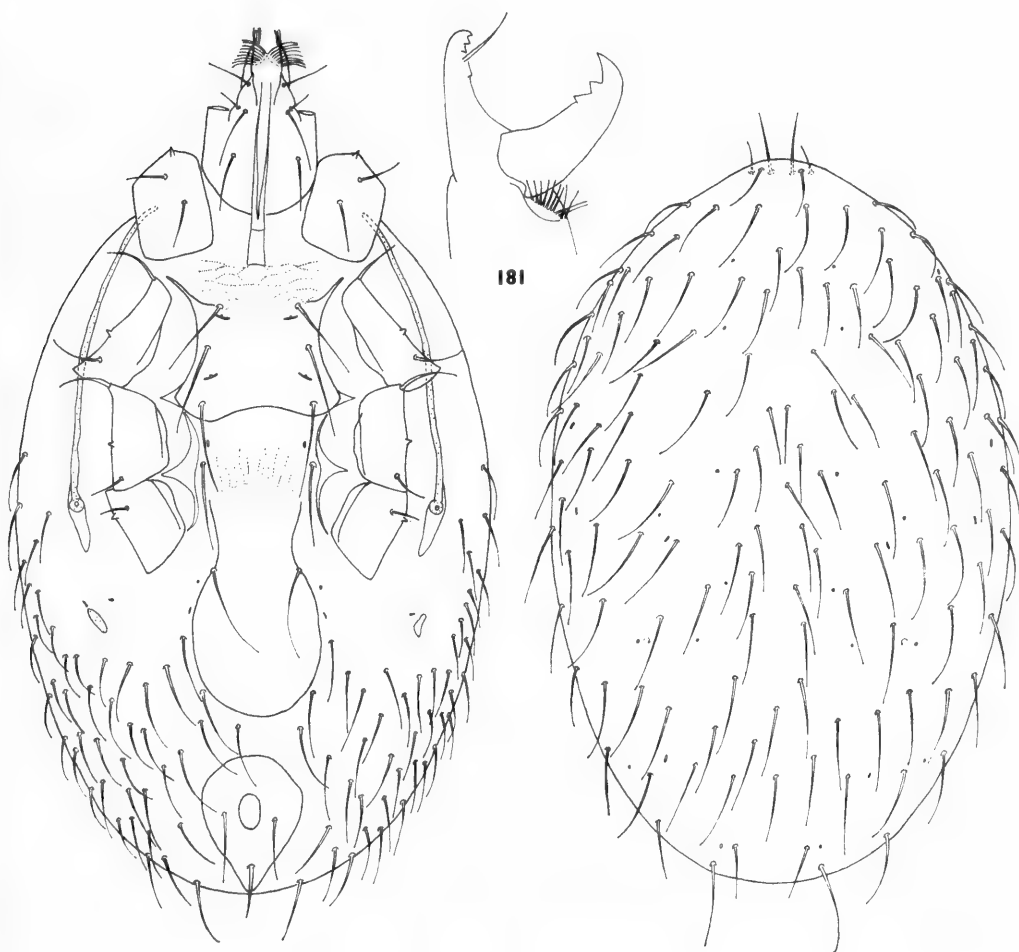
Dorsal shield oval, reticulate, showing pronounced hypertrichy which extends anterior to setae i_3 and which is not confined to the median part of the shield. The basic chaetotactic pattern is thus partially obscured. $DL=760-780\mu$; $DW=475-494\mu$; $DL/DW=1.5-1.6$.

Sternal shield reticulate, anterior margin not sharply defined. $SL=95-110\mu$; $SW=133-142\mu$; $SL/SW=0.7-0.8$. Sternal and metasternal setae subequal in length.

Genital shield flask-shaped, with a reticular pattern extending to the anterior flap. $GW_1=133-142\mu$; $GW_2=86-105\mu$; $GW_1/GW_2=1.4-1.5$. Genital setae as long as first pair of sternal setae and approximately equal to GW_2 .

Anal shield arched anteriorly. $AL=142-152\mu$; $AW=103-110\mu$; $AL/AW=1.4$.

Anus situated at approximately its length from the anterior margin of the shield. Paranal setae level with middle of anus, $1\frac{1}{4}$ times as long as the barbed postanal seta.



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FIGS. 179-181. *Androlaelaps walkerae* sp. nov., female. Venter (Fig. 179); dorsum (Fig. 180); chelicera (Fig. 181).

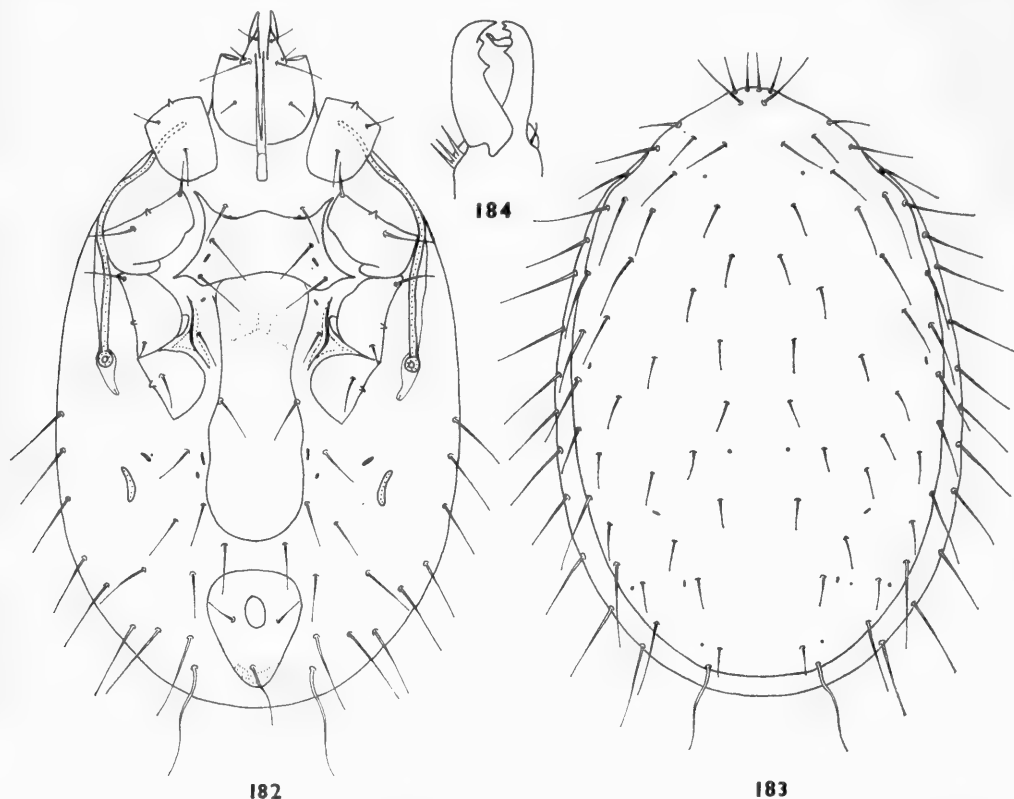
Integument of idiosoma provided with numerous setae, nearly all of which appear to be barbed. Metapodal plates oval or irregular in shape, length to width not more than 3 : 1.

Chaetotaxy of legs normal except that tibia I has 14 and tibia III has 9 setae. Tarsus II has 3 stout terminal and 3 stout ventral bristles, and many of the leg

setae are barbed. Posterior seta of coxa I slightly longer than anterior seta. Length of tarsus IV 7 times width at base.

MALE: Not known.

HOST AND LOCALITY: Sixty-three females from *Tachyoryctes splendens* (Rüppell), Muguga North, Kenya, 6 July, 1954, presented by Miss J. B. Walker, East African Veterinary Research Organization, to the South African Institute for Medical Research. Holotype and 38 paratypes in the collection of the S.A. Institute for



FIGS. 182-184. *Androlaelaps wilkini* (Till), female. Venter (Fig. 182); dorsum (Fig. 183); chelicera (Fig. 184).

Medical Research, 25 paratypes (1962.6.12.23-33) in the collection of the British Museum (Natural History).

Androlaelaps wilkini (Till)

Haemolaelaps wilkini Till, 1959, *J. ent. Soc. S. Afr.* 22 : 432, figs.

FEMALE (figs. 182-184): Deutosternum provided with 6 rows of 3-4 small teeth. Chelae about 40 μ long; pilus dentilis small, inflated; arthrodial filaments subequal in length.

Dorsal shield oval, reticulate; DL=709-770 μ ; DW=455-500 μ ; DL/DW=1.5-1.6,

The shield bears 37 pairs of setae, r_4 and r_6 being inserted on the adjacent integument. Marginal setae of the r and S series barbed, the S setae being at least twice as long and thick as those of the J series. Seta Z_5 sinuous, $2\frac{1}{2}$ –3 times as long as seta J_5 . Setae on the median part of the shield (i series posterior to i_3 , J series, z_2 – z_3 , Z_1 – Z_4 , px_2 – px_3) subequal in length, setae i_4 and z_2 slightly more than half as long as the distance between their bases.

Sternal shield and presternal area both reticulate. $SL=70$ – 79μ ; $SW=145$ – 158μ ; $SL/SW=0.5$. First pair of sternal setae slightly shorter than 2nd and 3rd pairs and situated on presternal area. Metasternal setae as long as first pair of sternal setae.

Genital shield relatively slender, very slightly widened behind the genital setae, lateral margins almost parallel, posterior portion with a reticulate pattern. $GW_1=123$ – 149μ ; $GW_2=96$ – 114μ ; $GW_1/GW_2=1.1$ – 1.3 .

Anal shield pear-shaped, with a reticulate pattern anteriorly and antero-laterally. $AL=123$ – 140μ ; $AW=114$ – 127μ ; $AL/AW=1.1$ – 1.2 . Paranal setae on a level between middle and posterior margin of anus, their length not more than $2/3$ that of the postanal seta.

Integument of idiosoma bears 24 pairs of ventral and marginal setae, the longer ones being provided with fine barbs; posterior terminal pair long and whip-like. Metapodal plates slender, slightly curved.

Tibia III has 9 setae; anterior and posterior setae on coxa I uniform in length and thickness. Tarsus II bears two blunt terminal spines; tarsi III and IV also have a pair of terminal spine-like bristles, but these are more slender and pointed than the spines on tarsus II. Length of tarsus IV 5 times width at base.

MALE: Not known.

HOSTS AND LOCALITIES: *Myrmecocichla formicivora* (Vieillot), Debeete, Bechuana-land (type series, S.A.I.M.R. and B.M.N.H.).

Merops apiaster Linnaeus, Johannesburg, Transvaal (S.A.I.M.R.).

Androlaelaps zulu (Berlese)

Hypoaspis (*Haemolaelaps*) *inops* var. *zulu* Berlese, 1918, *Redia* 13 : 125.

Haemolaelaps inops var. *zulu*, Keegan, 1956, *J. Egypt. publ. Hlth. Ass.* 31 : 234, fig. 18.

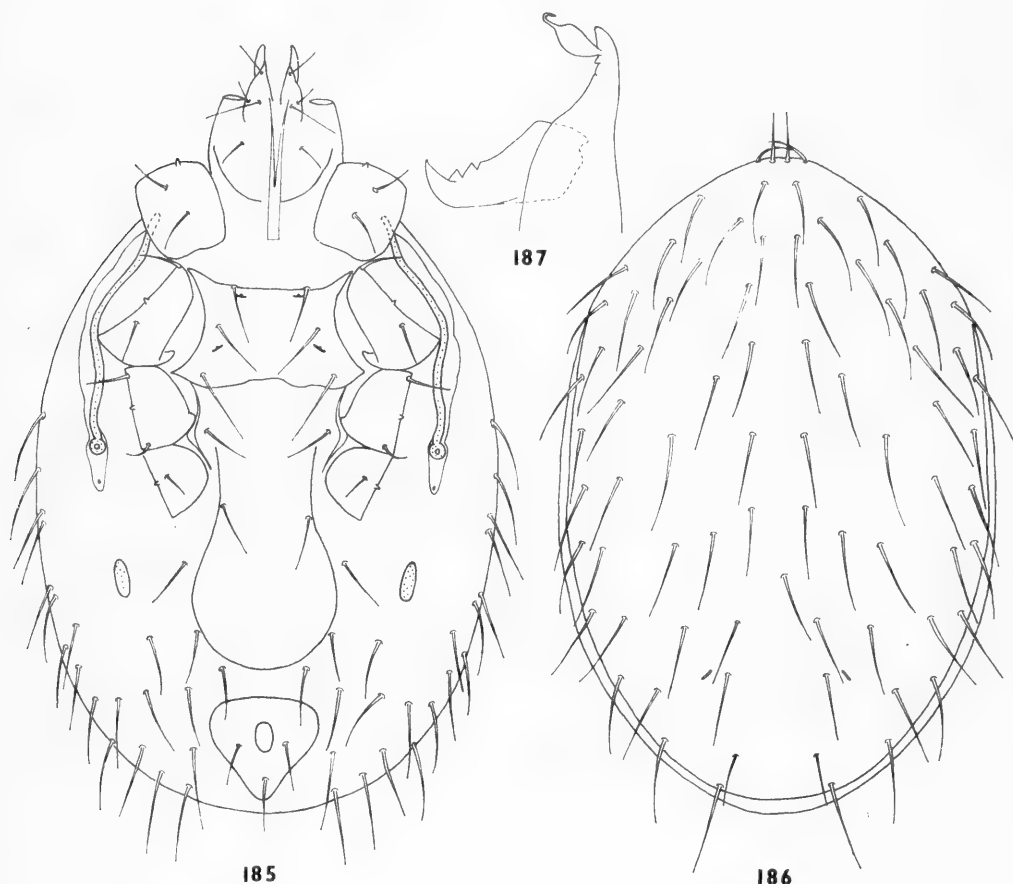
FEMALE (figs. 185–187): Deutosternum provided with 6 rows each of 4 narrow pointed teeth. Chelae 40μ long; pilus dentilis strongly inflated basally, distal third or fourth slender, with recurved apex; arthrodial filaments very short, subequal in length.

Dorsal shield reticulate, bearing 39 pairs of setae and 1–3 unpaired accessory setae between the J series. Setae on median part of shield relatively long, lengths of setae i_4 and z_2 about $1\frac{1}{2}$ times the distance between their bases. Marginal setae slightly longer and thicker, with fine barbs. Seta Z_5 at least $1\frac{1}{2}$ times as long as seta J_5 . $DL=627$ – 760μ ; $DW=400$ – 494μ ; $DL/DW=1.5$ – 1.6 .

Sternal shield reticulate, sharply demarcated from reticulate presternal area. $SL=100$ – 105μ ; $SW=128$ – 152μ ; $SL/SW=0.7$ – 0.9 . Metasternal setae about as long as first pair of sternal setae.

Genital shield reticulate, moderately expanded behind genital setae. $GW_1=143-170\mu$; $GW_2=105-114\mu$; $GW_1/GW_2=1.3-1.5$. Genital setae relatively short, slightly more than half GW_2 .

Anal shield reticulate antero-laterally. $AL=96-120\mu$; $AW=103-127\mu$; $AL/AW=0.9-1.0$. Anus situated less than its length from the anterior margin of the shield. Paranal setae between middle and posterior end of anus, reaching beyond base of, and about $4/5$ as long as, postanal seta.



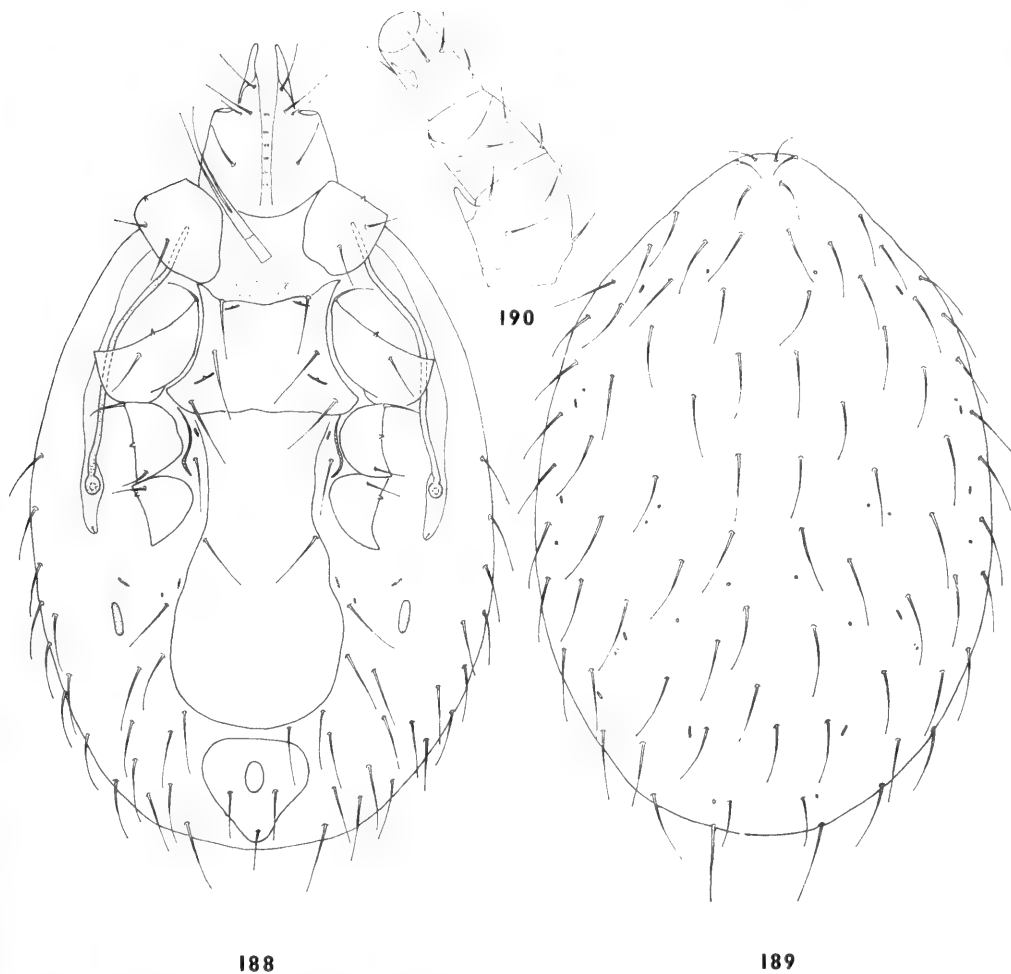
FIGS. 185-187. *Androlaelaps zulu* (Berlese), female. Venter (Fig. 185); dorsum (Fig. 186); chelicera (Fig. 187).

Integument of idiosoma bears about 22 pairs of marginal and ventral setae, of which 3 pairs border the genital shield. Marginal setae coarser than the truly ventral ones, and provided with fine barbs. Outer metapodal plates variable, usually cigar-shaped, length $2\frac{1}{2}-3\frac{1}{2}$ times the width.

Chaetotaxy of legs normal. Anterior seta on coxa I about $4/5$ as long as posterior seta. Length of tarsus IV at least 6 times width at base.

MALE: Not known.

HOSTS AND LOCALITIES: *Lemniscomys griselda* (Thomas), *Rattus natalensis* (Smith) and *Otomys irroratus* (Brants) from the Transvaal (S.A.I.M.R.).



FIGS. 188-190. *Androlaelaps zuluensis* Zumpt, female. Venter (Fig. 188); dorsum (Fig. 189); ventral view of femur, genu and tibia of leg II (Fig. 190).

Tatera afra (Gray) from Zululand (S.A.I.M.R.).

(Mites from the above hosts were previously identified by Zumpt & Till (1956) as forms of *Haemolaelaps glasgowi*.)

Keegan (1956) has recorded this species from several rodents in Egypt.

Androlaelaps zuluensis Zumpt

Hypoaspis (Androlaelaps) zuluensis Zumpt, 1950, *Parasitology* 40 : 300, fig. 1.

Turkiella zuluensis, Zumpt & Till, 1953, *Ann. Inst. Med. trop. Lisboa* 10 : 218, figs. 2-5.

Androlaelaps zuluensis, Keegan, 1956, *J. Egypt. publ. Hlth. Ass.* 31 : 229, fig. 14.

FEMALE (figs. 188-190): Deutosternum provided with 6 rows each of 3-4 very small teeth. Chelae 46μ long; pilus dentilis slender; arthrodial filaments short and subequal in length.

Dorsal shield reticulate, oval. $DL=656-675\mu$; $DW=403-486\mu$; $DL/DW=1.5$. The shield bears 39 pairs of setae as well as 2 or 3 unpaired accessory setae between the *J* series. Lengths of setae *i4* and *z2* approximately equal to the distance between their bases; seta *Z5* about $1\frac{1}{2}$ times as long as seta *J5*. The marginal setae appear to be barbed.

Sternal shield reticulate, posterior margin almost straight or slightly irregular. $SL=105\mu$; $SW=118-124\mu$; $SL/SW=0.9$. Sternal and metasternal setae all relatively short, a little more than half the length of the sternal shield.

Genital shield with a pattern of striations on its posterior portion; very long, extending almost to the anal shield. $GW_1=170\mu$; $GW_2=118-124\mu$; $GW_1/GW_2=1.4$. Genital setae very short, less than half GW_2 .

Anal shield with a reticulate pattern; $AL=105-109\mu$; $AW=105\mu$; $AL/AW=1.0$. Anus situated at less than its length from the anterior margin of the shield. Paranal setae near posterior margin of anus; postanal seta broken in both the specimens examined.

Integument of idiosoma bears 20-22 pairs of marginal and ventral setae. Metapodal plates slender, length 3-6 times the breadth.

Chaetotaxy of legs normal. Anterior seta on coxa I slightly shorter than posterior seta. Spur on femur II rather slender, thumb-like, its length a little less than half the width of the femur at its base. Inner ventral seta on genu II short, spur-like; inner ventral seta on tibia II considerably stouter than outer one; tarsus II terminates in pointed setae only. Length of tarsus IV about 8 times its width at the base.

MALE (fig. 191): Deutosternum with 6 rows of 2-5 small teeth. Spermadactyl 60μ long, fixed digit bears a slender pilus dentilis.

Dorsal shield similar to that of female; $DL=520\mu$ (approx.); $DW=360\mu$; $DL/DW=1.4$. Holoventral shield reticulate, expanded behind coxae IV, bearing 23 setae, 5 pairs of setae being situated in the preanal region behind coxae IV. Chaetotaxy of legs similar to that of female, except that inner ventral setae on genu II and tibia II are more slender.

HOSTS AND LOCALITIES: *Rattus namaquensis* (Smith) from Abercorn Pont, Zululand (holotype in S.A.I.M.R.), and from Kapps Siding, S. W. Africa (S.A.I.M.R.)

Rattus chrysophilus (De Winton), Southern Africa (Zumpt & Till, 1961).

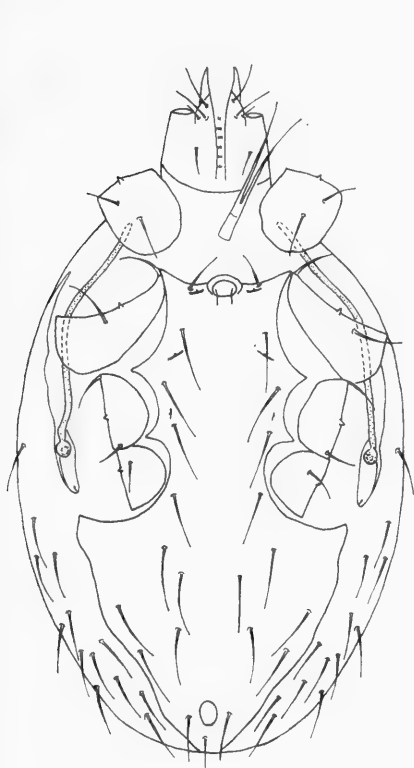
Petromyscus collinus (Thomas & Hinton), Kamanjab-Ohopoho Road, S.W. Africa (S.A.I.M.R.).

Galago senegalensis Geoffroy (the figured specimens) from Karamoja, Uganda (S.A.I.M.R.).

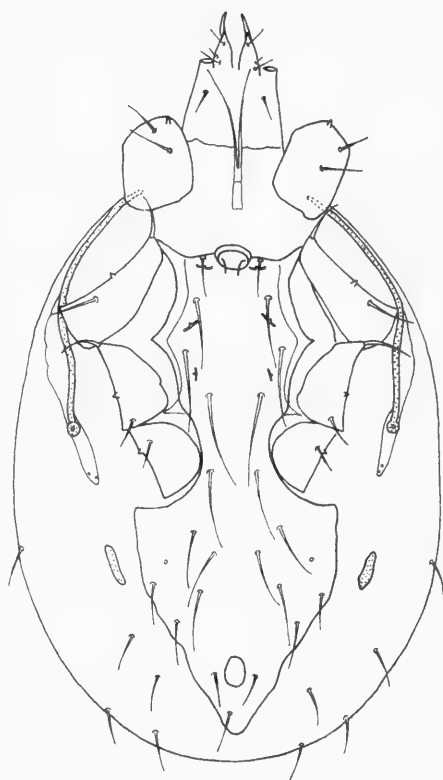
Keegan (1956) records this species from *Arvicanthis niloticus* (Desmarest) and *Mus musculus* Linnaeus in Egypt.

Androlaelaps zumpti sp. nov.

FEMALE (figs. 193-195): Deutosternum bears 6 rows of 3-5 very fine teeth. Chelae about 40μ long; pilus dentilis inflated; one arthrodial filament strikingly longer than the others; an extension of the arthrodial membrane between the chelae is elongate, reaching the tips of the chelae.



191



192

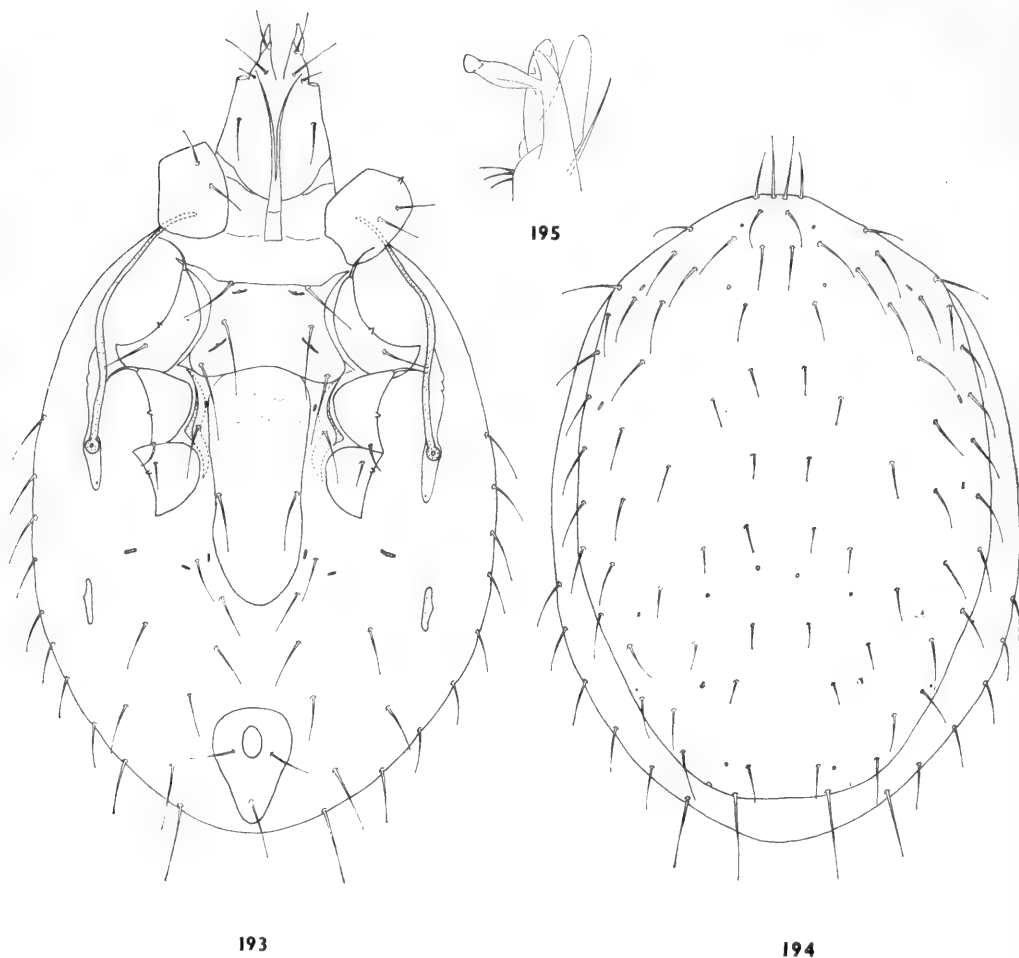
FIGS. 191-192. *Androlaelaps zuluensis* Zumpt, venter of male (Fig. 191).
Androlaelaps zumpti sp. nov., venter of male (Fig. 192).

Dorsal shield reticulate, widest in posterior half at level of setae S_1 and S_2 . $DL=656-732\mu$; $DW=442-494\mu$; $DL/DW=1.3-1.5$. The shield bears 39 pairs of setae; lengths of setae i_4 and z_2 a little more than half the distance between their bases; length of seta J_1 is $\frac{3}{4}$ that of seta S_1 ; seta Z_5 is $2-2\frac{1}{2}$ times as long as seta J_5 .

Sternal shield reticulate, sharply demarcated from reticulate and granular presternal area. $SL=86-114\mu$; $SW=124-133\mu$; $SL/SW=0.7-0.9$. Metasternal

and first pair of sternal setae subequal in length, 2nd and 3rd pairs of sternal setae slightly longer.

Genital shield scarcely widened behind genital setae, tapering posteriorly, with a well-defined reticular pattern extending over the anterior as well as posterior parts.



FIGS. 193-195. *Androlaelaps zumpti* sp. nov., female. Venter (Fig. 193); dorsum (Fig. 194); chelicera (Fig. 195).

$GW_1=95-114\mu$; $GW_2=95-105\mu$. Genital setae about as long as first pair of sternal setae and about $2/3$ GW_2 .

Anal shield about 133μ long, 90μ wide; $AL/AW=1.5$. Anus situated at less than its length from the anterior margin of the shield. Paranal setae near posterior margin of anus, about $2/3$ as long as postanal seta.

Integument of idiosoma bears about 23 pairs of ventral and marginal setae, those

near the posterior extremity of the body having fine barbs. Metapodal plates slender, length at least 5 times the width.

Chaetotaxy of legs normal, anterior seta on coxa I about 4/5 as long as posterior seta. Trochanter IV bears a stout dorsal seta. Length of tarsus IV about 6 times its width at the base.

MALE (fig. 192): Deutosternum bears 6 rows of 4-7 very fine teeth. Fixed digit of chelicera bears a pilus dentilis similar in shape to that of the female.

Dorsal shield 550 μ long, 352 μ wide; chaetotaxy similar to that of female. Holoventral shield strongly reticulate, bearing 23 setae, 5 pairs being placed in the region between coxae IV and the anus. Chaetotaxy of legs as in the female.

HOSTS AND LOCALITIES: Holotype (female), allotype and one male and three female paratypes from *Rattus (Aethomys)* sp., Richmond, Cape Province, 31 March, 1959, two female paratypes from *Rattus (Aethomys)* sp., Middelburg, Cape Province, 28 March, 1959. Holotype, one male and two female paratypes in the collection of the South African Institute for Medical Research; allotype (1962.6.12.34) and two female paratypes (1962.6.12.35-36) in the collection of the British Museum (Natural History).

NOTE: Several populations of mites have been examined which are very similar to *A. zumpti*, except that the setae of the dorsal shield are longer (lengths of setae *i*₄ and *z*₂ about 1½ times the distance between their bases) and 2-4 accessory setae are present. These mites, all from the collection of the S.A. Institute for Medical Research, have been taken from the following hosts and localities:—

Rattus chrysophilus (De Winton), Matopos, S. Rhodesia.

Rattus namaquensis (Smith), Bulawayo, S. Rhodesia; Abercorn Pont, Zululand; several localities in S.W. Africa.

Rattus paedulcus (Sundevall), Kaokoveld, S.W. Africa.

Otomys unisulcatus Cuvier, Luckhoff, Orange Free State.

Rhabdomys pumilio (Sparrman), Cape Province and S.W. Africa.

Petromyscus collinus (Thomas & Hinton), Kamanjab-Ohopoho, S.W. Africa.

Specimens from *Parotomys littledalei* Thomas, van Rhynsdorp, Cape Province, are intermediate between these and the short-haired form, the lengths of setae *i*₄ and *z*₂ being slightly less than the distance between their bases. For the present, these will all be regarded as forms of *A. zumpti*.

HOST-PARASITE LIST.*

CLASS AVES

Order FALCONIFORMES

FAMILY AEGYPIIDAE

Gyps coprotheres (Forster)

Androlaelaps patersoni (Zumpt & Till)

* The host names are the same as those used by Zumpt (1961).

Order **CORACIIFORMES**FAMILY **MEROPIDAE****Merops apiaster** Linnaeus*Androlaelaps wilkini* (Till)FAMILY **PHOENICULIDAE****Phoeniculus purpureus** (Miller)*Androlaelaps phoeniculi* (Zumpt & Till)FAMILY **CAPITONIDAE****Lybius torquatus** (Dumont)*Androlaelaps steyni* (Till)**Trachyphonus vaillanti** Ranzani*Androlaelaps steyni* (Till)FAMILY **PICIDAE****Campethera abingoni** (Smith)*Androlaelaps haydocki* (Till)**Thripias namaquus** (Lichtenstein)*Androlaelaps haydocki* (Till)**Mesopicos griseocephalus** (Boddaert)*Androlaelaps mesopicos* (Radford)Order **PASSERIFORMES**FAMILY **TURDIDAE****Myrmecocichla formicivora** (Vieillot)*Androlaelaps wilkini* (Till)FAMILY **HIRUNDINIDAE****Riparia paludicola** (Vieillot)*Androlaelaps spreo* (Zumpt & Till)FAMILY **STURNIDAE****Lamprotornis nitens** (Linnaeus)*Androlaelaps steyni* (Till)**Spreo bicolor** (Gmelin)*Androlaelaps spreo* (Zumpt & Till)FAMILY **PLOCEIDAE****Spermestes cucullatus** Swainson*Androlaelaps congoensis* sp. nov.CLASS **MAMMALIA**Order **INSECTIVORA**FAMILY **MACROSCOLIDIDAE**

Elephant Shrew

Androlaelaps arvicantis RadfordFAMILY **SORICIDAE****Suncus varius** (Smuts)*Androlaelaps suncus* sp. nov.

Crocidura spec.

Androlaelaps suncus sp. nov.

Crocidura manni Peters

(?) *Androlaelaps hystrici* (Zumpt & Till)

Order **PRIMATES**

FAMILY **LORISIDAE**

Galago alleni Waterhouse

Androlaelaps galagus (Lavoipierre)

Galago senegalensis Geoffroy

Androlaelaps zuluensis Zumpt

Order **CARNIVORA**

FAMILY **MUSTELIDAE**

Ictonyx striatus (Perry)

Androlaelaps marshalli Berlese

FAMILY **VIVERRIDAE**

Suricata suricatta (Schreber)

Androlaelaps marshalli Berlese

Order **LAGOMORPHA**

FAMILY **LEPORIDAE**

Oryctolagus cuniculus (Linnaeus)

Androlaelaps marshalli Berlese

Order **RODENTIA**

FAMILY **BATHYERGIDAE**

Bathyergus suillus (Schreber)

Androlaelaps scapularis (Berlese)

Georchus capensis (Pallas)

Androlaelaps capensis (Hirst)

Androlaelaps cryptomius (Radford)

Androlaelaps georchyi sp. nov.

Cryptomys holosericeus (Wagner)

Androlaelaps capensis (Hirst)

Androlaelaps scapularis (Berlese)

Cryptomys hottentotus (Lesson)

Androlaelaps capensis (Hirst)

Androlaelaps marshalli Berlese

Androlaelaps scapularis (Berlese)

Cryptomys mechowii Peters

Androlaelaps tauffliebi sp. nov.

FAMILY HYSTRICIDAE**Hystrix cristata** Linnaeus*Androlaelaps hystrici* (Zumpt & Till)**FAMILY SCIURIDAE****Sciurus carolinensis** Gmelin*Androlaelaps casalis* (Berlese)**Heliosciurus gambianus** (Ogilby)*Androlaelaps heliosciuri* sp. nov.**Xerus inauris** (Zimmermann)*Androlaelaps casalis* (Berlese)**FAMILY ANOMALURIDAE****Anomalurus derbianus** (Gray)*Androlaelaps spatuliformis* (Lavoipierre)**FAMILY PEDETIDAE****Pedetes capensis** (Forster)*Androlaelaps marshalli* Berlese**FAMILY MUSCARDINIDAE****Claviglis** spec.*Androlaelaps ghanensis* sp. nov.**FAMILY RHIZOMYIIDAE****Tachyoryctes** spec.*Androlaelaps callosus* (Berlese)**Tachyoryctes splendens** (Rüppell)*Androlaelaps marshalli* Berlese*Androlaelaps tachyoryctes* (Radford)*Androlaelaps walkerae* sp. nov.**FAMILY MURIDAE****Arvicanthis niloticus** (Desmarest)*Androlaelaps arvicanthis* Radford*Androlaelaps marshalli* Berlese*Androlaelaps murinus* (Berlese)**Rattus** spec.*Androlaelaps zumpti* sp. nov.**Rattus chrysophilus** (De Winton)*Androlaelaps dasymys* (Radford)*Androlaelaps marshalli* Berlese*Androlaelaps taterae* (Zumpt & Patterson)*Androlaelaps theseus* Zumpt*Androlaelaps zuluensis* Zumpt*Androlaelaps zumpti* sp. nov.**Rattus morio** (Trouessart)*Androlaelaps rhodesiensis* (Zumpt & Patterson)**Rattus namaquensis** (Smith)*Androlaelaps dasymys* (Radford)*Androlaelaps marshalli* Berlese

Androlaelaps zuluensis Zumpt

Androlaelaps zumpti sp. nov.

Rattus natalensis (Smith)

Androlaelaps arvicanthi Radford

Androlaelaps dasymys (Radford)

Androlaelaps marshalli Berlese

Androlaelaps murinus (Berlese)

Androlaelaps taterae (Zumpt & Patterson)

Androlaelaps theseus Zumpt

Androlaelaps zulu (Berlese)

Rattus paedulcus (Sundevall)

Androlaelaps marshalli Berlese

Androlaelaps zumpti sp. nov.

Rattus rattus (Linnaeus)

Androlaelaps casalis (Berlese)

Androlaelaps dasymys (Radford)

Androlaelaps rhodesiensis (Zumpt & Patterson)

Rhabdomys pumilio (Sparrman)

Androlaelaps dasymys (Radford)

Androlaelaps glasgowi (Ewing)

Androlaelaps marshalli Berlese

Androlaelaps murinus (Berlese)

Androlaelaps zumpti sp. nov.

Lophuromys flavopunctatus Thomas

Androlaelaps callosus (Berlese)

Androlaelaps murinus (Berlese)

Lophuromys sikapusi (Temminck)

Androlaelaps dasymys (Radford)

Oenomys hypoxanthus (Pucheran)

Androlaelaps murinus (Berlese)

Dasymys incomtus (Sundevall)

Androlaelaps dasymys (Radford)

Androlaelaps murinus (Berlese)

Lemniscomys griselda (Thomas)

Androlaelaps marshalli Berlese

Androlaelaps zulu (Berlese)

Lemniscomys striatus (Linnaeus)

Androlaelaps murinus (Berlese)

Androlaelaps tachyoryctes (Radford)

Acomys cahirinus (Desmarest)

Androlaelaps theseus Zumpt

Saccostomus campestris Peters

Androlaelaps marshalli Berlese

Androlaelaps oliffi (Zumpt & Patterson)

Androlaelaps rhodesiensis (Zumpt & Patterson)

- Androlaelaps theseus* Zumpt
Androlaelaps villosissimus (Berlese)
- Cricetomys gambianus** Waterhouse
Androlaelaps cricetomydis sp. nov.
Androlaelaps galagus (Lavoipierre)
- Petromyscus collinus** (Thomas & Hinton)
Androlaelaps zuluensis Zumpt
Androlaelaps zumpti sp. nov.
- Steatomys pratensis** Peters
Androlaelaps marshalli Berlese
Androlaelaps rhodesiensis (Zumpt & Patterson)
Androlaelaps theseus Zumpt
- Otomys** spec.
Androlaelaps murinus (Berlese)
- Otomys irroratus** (Brants)
Androlaelaps dasymys (Radford)
Androlaelaps glasgowi (Ewing)
Androlaelaps murinus (Berlese)
Androlaelaps taterae (Zumpt & Patterson)
Androlaelaps zulu (Berlese)
- Otomys saundersiae** Roberts
Androlaelaps dasymys (Radford)
- Otomys sloggetti** (Thomas)
Androlaelaps dasymys (Radford)
- Otomys unisulcatus** Cuvier
Androlaelaps zumpti sp. nov.
- Parotomys brantsi** (Smith)
Androlaelaps dasymys (Radford)
- Parotomys littledalei** Thomas
Androlaelaps dasymys (Radford)
Androlaelaps zumpti sp. nov.
- Mystromys albicaudatus** (Smith)
Androlaelaps capensis (Hirst)
Androlaelaps dasymys (Radford)
- Desmodillus auricularis** (Smith)
Androlaelaps marshalli Berlese
Androlaelaps oliffi (Zumpt & Patterson)
- Gerbillus paebe** Smith
Androlaelaps marshalli Berlese
Androlaelaps oliffi (Zumpt & Patterson)
- Gerbillus pyramidum** Geoffroy
Androlaelaps centrocarpus (Berlese)
- Meriones rex** Yerbury & Thomas
Androlaelaps longipes (Bregetova)

Tatera spec.*Androlaelaps arvicanthis* Radford*Androlaelaps marshalli* Berlese**Tatera afra** (Gray)*Androlaelaps dasymys* (Radford)*Androlaelaps marshalli* Berlese*Androlaelaps oliffi* (Zumpt & Patterson)*Androlaelaps taterae* (Zumpt & Patterson)*Androlaelaps theseus* Zumpt*Androlaelaps zulu* (Berlese)**Tatera nigricauda** Peters*Androlaelaps marshalli* Berlese*Androlaelaps tateronis* (Radford)**Tatera valida** (Bocage)*Androlaelaps arvicanthis* Radford*Androlaelaps marshalli* Berlese*Androlaelaps tateronis* (Radford)**Taterillus spec.***Androlaelaps centropus* (Berlese)**Taterillus emini** (Thomas)*Androlaelaps marshalli* Berlese

Unidentified rodents

Androlaelaps arvicanthis Radford*Androlaelaps graingeri* Zumpt & Patterson*Androlaelaps hirsti* (Keegan)*Androlaelaps marshalli* Berlese*Androlaelaps tateronis* (Radford)*Androlaelaps villosissimus* (Berlese)

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INTRODUCTION

Thirty-nine species of francolin (*Francolinus* and *Pternistis*) were recognised in Peters' Check List of the Birds of the World 2, 1934, of which thirty-four are African and five Asiatic: one (*F. ochropectus* Dorst & Jouanin, 1952) has been described since. I have rearranged Peters' species slightly, now recognising thirty-six in Africa and five in Asia. As is inevitable a Check List employing conventional nomenclature gives no indication of the relationship between the species which must be the basis for any discussion on speciation. The objectives of this paper are therefore twofold: firstly to set out in the text and on the maps the present relationship between the species. This is not as formidable a task as might be expected

from the number of species involved, for thirty-seven of the forty-one fall readily into eight groups, seven of which are African and one Asiatic. (In this paper the term "group" is used for either a superspecies, in which all members are largely allopatric, or for a species group which is a rather looser assemblage of related forms containing some species which are partly sympatric with other members.) These groups are discussed and mapped separately with particular reference to their ecology and the relationship of neighbouring or sympatric forms. The four species that do not fall readily into any group are discussed separately at the end.

Secondly, from the pattern presented by the birds of each group and by their distribution I have tried to reconstruct the climatic changes, with the resultant isolating and rejoining of populations, which could have formed this pattern. In doing so I am fully conscious that the picture we see today gives only fragmentary clues to the past and that it is impossible to interpret accurately any but the simplest situations. Nevertheless, even in the most complex groups, I believe there is some usefulness in making the attempt, for if a series of studies of this nature suggests changes that from other branches of science are known to have occurred, it may be possible to give some tentative datings to various steps in speciation.

Throughout the preparation of this paper I have been particularly fortunate in being able to discuss the problems with R. E. Moreau, who has been preparing concurrently a paper on "The Vicissitudes of the African Biota in the Late Pleistocene". He has allowed me to quote as Appendix 1 a summary of his conclusions of the major climatic changes that have taken place in Africa in the past 60,000 years. In acknowledging my gratitude to him for this and for invaluable advice and criticism I must also absolve him from any responsibility for some of my interpretations of the evolutionary stages, or the conclusions which I have drawn from them.

I am also deeply indebted to M. P. Stuart Irwin who prepared distribution maps for me of all the francolins in the National Museum of Southern Rhodesia: also to Dr. H. Friedmann, C. W. Benson and I. C. J. Galbraith for criticism of the manuscript. Others to whom I am grateful for loans of specimens, advice, or other help, include Dr. Dean Amadon, Professor J. Berlioz, P. Blasdale, Mgr. F. O. Cave, E. M. Cawkell, Dr. James Chapin, P. A. Clancey, Miss M. Courtenay-Latimer, I. H. Dillingham, H. J. de S. Disney, Sir Hugh Elliot, W. V. Harris, M. J. Hollis, Cdr. A. M. Hughes (who drew figure 1), Gen. Sir Gerald Lathbury, C. W. Mackworth-Praed, Miles Markus, Col. R. Meinertzhagen, Captain C. R. S. Pitman, O. P. M. Prozesky, Professor H. Schouteden, Rev. Dr. W. Serle, R. H. N. Smithers, B. W. H. Stronach, M. A. Traylor, Dr. C. Vaurie, Col. Jack Vincent, Professor V. Van Straelen, John Williams, Dr. J. M. Winterbottom.

THE GENUS

The francolins are recognised as a branch of the sub-family Phasianinae (Partridges, Quails, Pheasants) which comprises over fifty genera, most of which are Palaearctic or Asiatic. My interest for this paper is primarily in the African members of the genus, but the five Asiatic species are included since they provide

some interesting points of comparison. I am not, however, competent to enter into a discussion on the limitations of the genus in Asia where there are thirty-eight other genera in the same sub-family some of which such as *Rhizothera*, *Alectoris*, *Perdix*, *Arboricola* seem closely related to *Francolinus*. They have been distinguished on various structural characters such as the number of tail-feathers, the size and shape of the bill, or the length of tail, and I have accepted these distinctions uncritically. It is sufficient to say that the francolins are characterised by a rather longer, more hooked bill than members of the other genera (except *Rhizothera*), a short tail of fourteen feathers, and an upright stance: in the majority of species the male, at least, is spurred. The range of colours in the plumage is limited to the shades of ochre, chestnut, brown, black and white produced by melanic pigments, but the pattern of individual feathers is complex and varied.

The partridge of Madagascar, *Margaroperdix*, has also some similarity to the francolins (particularly to the forest francolin *F. lathamii*) in colour and pattern, but has various structural differences in bill, tail and legs, which make it doubtful if the two are very closely related. Apart from this in the Ethiopian region there are no gamebirds that can be regarded as similar to francolins in either structure or habits, the only others being the quails (*Coturnix* and *Excalfactoria*), the Stone Partridge (*Ptilopachus*)—a bird confined to the savanna and steppe belt north of the Equator—the Congo Peacock (*Afropavo*), confined to the Congo forest, and the guinea-fowl family (Numididae).

I would suggest therefore that the closer affinities of *Francolinus* with Palaearctic and Asiatic genera indicate that it originated in Asia, becoming separated from the other game-birds as a species particularly adapted to sub-tropical grasslands, and that later it spread into southern Europe and Africa. Once in Africa lack of efficient competition allowed it to spread widely and to exploit varied habitats which, in Asia, are occupied by other related genera.

If this hypothesis of the origin of *Francolinus* is accepted it is apparent that there are factors present in Africa that have encouraged speciation in the comparatively recent past (since the emergence of the genus). This is readily acceptable in view of the climatic changes known to have taken place (see Appendix 1). Fluctuations in humidity and temperature would cause redistribution of the montane and lowland forests, and the woodlands, savannas and steppes, isolating and rejoining the populations of their indigenous birds.

Among the francolins various generic divisions have been proposed, the most commonly accepted being *Pternistis* for the bare-throated francolins (as in Peters', 1934: 84). However, I agree with White (1952) that the bare throat alone is not a generic character and in other respects these birds are closer to some of the other large francolins than are other members of the genus. If a generic division was to be made I would separate the birds of the first five groups (including the Bare-Throated Group) which have relatively plain or vermiculated backs, from the birds of the last three groups with striated or quail-type patterning on the backs, placing *F. gularis* with the former and *F. pondicerianus* and *F. lathamii* with the latter. However, I regard such a division as unnecessary and leading to difficulties in respect of the rather atypical species *F. nahani*.

For a study on speciation francolins have the advantage of being remarkably sedentary birds for their size, not disposed to fly any great distances, and closely associated with a particular habitat. Morphologically the bold colours and patterns, particularly on the underparts, have the advantage of indicating where interbreeding has or has not taken place between neighbouring forms. Finally their "sporting" and edible qualities have given them an interest to many people other than ornithologists so that their ranges and habits are probably rather better known than those of any comparable group: at the same time these qualities have led to a persecution of the genus over the last fifty years which, combined with the damage done by intensive agriculture to the natural habitats, has almost exterminated species from some areas in which they were common and renders it difficult, if not impossible, to get further information about the habits of species from some areas which are now "developed".

THE GROUPS

Grouping the francolins has presented little difficulty, for the close relationship of most members is evident from their appearance, ecology and distribution and has been recognised by previous authors. In a few cases where the relationship is less obvious this is discussed in the text. I have felt that it facilitates discussion to give descriptive names to the groups rather than numbers, and the names chosen indicate an important character common to all members though it has not been possible in all cases to find a character which is exclusive to the group.

The order in which the groups are listed and discussed is not intended to be systematic except that the first five and the last three appear to form related assemblages.

The groups and the species that comprise them are as follows:—

1. Spotted Group (*francolinus*, *pictus*, *pintadeanus*).
2. Bare-throated Group (*afer*, *swainsonii*, *rufopictus*, *leucoscepus*).
3. Montane Group (*erckelii*, *ochropectus*, *castaneicollis*, *jacksoni*, *nobilis*, *camerunensis*, *swierstrai*).
4. Scaly Group (*ahantensis*, *squamatus*, *griseostriatus*).
5. Vermiculated Group (*bicalcaratus*, *icterorhynchus*, *clappertoni*, *hildebrandti natalensis*, *hartlaubi*, *harwoodi*, *adpersus*, *capensis*).
6. Striated Group (*sephaena*, *streptophorus*).
7. Red-winged Group (*psilolaemus*, *shelleyi*, *africanus*, *levaillantoides*, *levaillantii*, *finschi*).
8. Red-tailed Group (*coqui*, *albogularis*, *schlegelii*).

The four species not assigned to any group are the two African forest francolins *lathamii* and *nahani*, and the two Asiatic species *pondicerianus* and *gularis*.

SPECIES AND SUBSPECIES

In discussing speciation it must always be borne in mind that this is a continuous divergent progress starting when two populations become isolated from each other. In isolation each will develop divergent characters, either morphological or ecological, or both, but there will be a long period during which the two populations are

sufficiently alike for free interbreeding to take place if the isolating barrier is removed (Phase 1). If they remain isolated and divergence continues this stage will gradually merge into one in which the divergent characters become such that interbreeding is unlikely (but not impossible) if the two populations rejoin (Phase 2). Again these characters may be ethological, involving different recognition patterns or voice; or ecological, so that the two are unlikely to occur on the same ground; or could possibly be a difference in breeding seasons. It is in this stage that the occasional hybrid may be produced in the wild, and in which hybridisation is possible and frequent under artificial conditions. Finally the two birds diverge so completely that they are incapable of interbreeding (Phase 3).

In general most populations in Phase 1 and in the transition period between Phase 1 and 2 would be regarded as subspecies and those in Phase 2 and 3 as species, but there is no line between them and the decision must rest on the assessment of the taxonomist. This must be based on the degree of divergence and the degree to which they are known to interbreed. In the francolins members of different groups may be assumed to have reached, or almost reached, Phase 3 in their relationship, but the allopatric members of each group may be only in Phases 1 and 2.

Each group provides a case in which I have had to make an arbitrary decision whether or not to regard neighbouring forms as conspecific. For example, in the Spotted Group *F. francolinus* and *F. pictus* have diverged appreciably, especially in males, and hybrids are scarce, so I treat them as species. In the Bare-throated Group the *afer* block and the *cranchii* block have also diverged but interbreed freely, so are treated as conspecific. In the Montane Group *F. ochropectus* has diverged morphologically and ecologically from *F. erckelii* and is isolated, so is treated as a species, while *atrifrons* stands in a similar morphological relationship to *castaneicollis* but has the same field habits so is considered conspecific. In the Scaly Group the Niger provides a barrier between *F. ahantensis* and *F. squamatus* so it is not certain if they are capable of interbreeding but they seem to have diverged sufficiently to justify specific status. In the Vermiculated Group *F. hildebrandti* and *F. natalensis* have diverged, especially in the females, but interbreed to a limited extent at one point of contact but not apparently at another so are treated as species. In the Striated Group "*rovuma*" type birds (with a streaked abdomen) apparently do not interbreed with "*sephaena*" types (unstreaked) in the southern half of the range but hybridise in the north; the divergence is slight, however, and they are treated as conspecific. In the Red-winged Group the degree of divergence and the relationship between *shelleyi* and its three neighbours, *africanus*, *whytei*, and *uluensis* varies only slightly, but is just sufficient for me to treat *africanus* as a species and the other three as conspecific. In the Red-tailed Group the northern forms of *coqui* have diverged slightly, both morphologically and ecologically, from the southern but seem capable of interbreeding so must be considered conspecific.

The foregoing demonstrates the impossibility of defining a species in such conditions. For this reason I have tried to avoid differentiating strongly between species and subspecies in the discussion, though greater clarity might have been achieved by setting out the discussion under specific headings (as has been done in the Red-winged Group where rearrangement of the species made it necessary).

On the other hand I have endeavoured to make a clear distinction between those subspecies which I term "potential species"—namely those which are either (a) isolated at present, or (b) must be assumed to have been isolated at some period, since they show a degree of divergence from their neighbours which is too great to be attributable to local ecological factors—and those subspecies whose divergence can be attributed to ecological factors and which, as a rule, form part of a cline. The characters and ranges of "potential species" are defined equally with those of full species, but other subspecies are noted summarily in smaller print in a section in each group headed "Other variation", together with any significant local or individual variation. On the maps as much information as possible has been shown on the ranges and relationships of species and subspecies, but this has necessarily been dependent on the complexity of each map. However, I do not consider it practical or desirable to recognise numerous steps in a cline, or slight local variations, and have relegated to the synonymy many names given to such intermediates and micro-populations. There is more justification in naming isolated populations, however small, such as some of the montane ones, and in these cases I have been guided by the degree of divergence shown. For instance, I regard names as desirable for such highly divergent small populations as the montane francolins found on the Plateau du Day in (French) Somaliland (*ochropectus*) and at Mega in southern Abyssinia (*atrifrons*), but not for others in the same group in other mountains of southern Abyssinia which differ only slightly from each other. To avoid encumbering the main discussion with irrelevant detail, notes on taxonomy and synonymy are confined to an appendix.

In the parts of the paper dealing with evolution the ancestral stock of present species or of more than one species is referred to with the prefix "proto" (e.g. *proto-coqui* and *proto-albogularis/schlegelii*): if clarity demands, the name is followed by "subsp." or "sp.". The name of the author and date of publication are inserted only for those subspecies not listed by Peters (1934).

METHODS

The extensive collection of francolins in the British Museum has formed the basis for this study, supplemented by loans of critical specimens from other museums. All the African specimens examined and all the authentic records I have been able to trace in literature have been plotted over the Vegetation Map of Africa (Oxford 1959), as many species as possible being entered on a single sheet. This has enabled me to make a direct comparison of the range of any species with the vegetational belts and with the range of other species, whether in the same group or not. The Asiatic species have been plotted with accuracy only in the few critical areas, and for this the distribution maps of Indian birds prepared by Whistler, but never published, have been of great assistance. The maps of the groups have been compiled from these key maps. In a distribution map it is always difficult to know to what extent the range should be shown as continuous between actual collecting points, and in this respect the maps differ. For the Asiatic species I have shown the

limits of the range only: for the African species I have, as a general rule, shaded only areas from which specimens have been obtained, though this may give a rather distorted picture from parts of the country which are least known ornithologically: in a few cases, most notably for the Bare-throated Francolins (Map 2), I have felt that greater clarity in presentation could be achieved by shading the whole area within the limits of the range: this has been done only with species which, from their known habitat preferences, could be expected to have a reasonably continuous distribution within a vegetation belt.

The morphological discussion is based on specimens examined personally unless otherwise stated. For the field notes I have used the standard regional works as a basis but these have been immeasurably enriched by the numerous conversations and letters that I have exchanged with the many field workers whose names appear in the acknowledgments. Where these workers have been responsible for specialised information I have tried to give the credit in the text, but they are responsible also for much of the general information which is incorporated without acknowledgment.

I have found it difficult when discussing ecology and habitat to be consistent in the descriptive terms used, especially in correlating the parts of southern Africa with which I am familiar with those of the north for which I have to rely on the descriptions of others. As far as possible I have followed the terminology employed by the Vegetation Map of Africa (Map 11). In this the vegetational types which mainly concern the francolins are the Woodlands, Savannas and Steppes (Types 16-25). My own experience in southern Africa and the works of such specialists in ecology as Benson and Stuart Irwin show the importance of the distinction between the woodlands in which acacia is rare or absent (the "brachystegia woodlands" or "myombo"—Types 18 and 19) and the acacia country, whether it is termed acacia "woodland", "savanna" or "steppe". This distinction applies not only to the birds of the actual woodlands but also to those of the grasslands and savannas (i.e. grasslands with scattered trees) with which the woods are interspersed, many birds being strictly confined to either the brachystegia belt or to acacia. (In the southern and eastern francolins there are, in fact, several species indigenous to acacia, such as *F. sephaena*, *F. leucoscepus*, *F. rufopictus*, *F. adspersus* and *F. levaillantoides*, but none which is wholly indigenous to the woodland belt, though the potential species *F. s. shelleyi* and *F. s. whytei* and the Bare-throated *F. afer* nearly qualify.) I have therefore made a clear distinction in the discussions between the brachystegia belt and acacia country and throughout the paper the term "woodland" is used exclusively for types 17-19 unless "acacia woodland" is specifically stated.

North of the equatorial forest the woodlands are apparently similar in character to the brachystegia woodlands though composed largely of different species of trees and less continuous (Type 17). I am told also that, because of this discontinuity, the transition from the woodland belt to the acacia is less clearly defined. It is to be expected that there are therefore less clear-cut ecological distinctions in the birds, but this is not easy to determine from published works, the term "savanna" being widely used by different authors without clear definition. I have therefore been less precise in discussing the habitat of northern francolins. (From the maps it

appears that *F. clappertoni* and *F. coqui spinetorum* may be indigenous to acacia, and *F. schlegelii*, *F. albogularis* and *F. icterorhynchus* to the woodland belt.)

The distinction between acacia "woodlands", "savannas" and "steppes" is largely one of aridity and the transition between the types is necessarily gradual. It will be appreciated from the foregoing that savannas are found in both the woodland and acacia belts, but they are necessarily different in character. Where the term is used without qualification it should be plain from the context which belt is under discussion.

In attempting to interpret in terms of evolution the pattern presented in each group by divergence, ecology and ranges, I have started in each case with the distributional maps. From these I have tried to find in each group the factor that limits the ranges. More often than not the answer lies in the vegetation map, and the range of a group, species or potential species will be found to coincide with the limits of a vegetation belt, this coincidence being particularly common where acacia savanna or steppe changes to woodland. The presence or absence of mountains, hills or rivers is obviously significant in other cases, but here it must be remembered that, while the reason for the present discontinuity in the range of a species may be self-evident, the range must have been continuous in the comparatively recent past. In one case, the Red-winged Group, the limits of ranges of species coincide not so much with the vegetational belts as with the isohyets of total annual rainfall. In another, the Striated Group, the isolated areas from which one species (*F. streptophorus*) is found seem to have nothing in common except that they are the two ends of a ridge of higher country. In several cases where there seems no ecological reason for the limits of a species' range the bird is replaced by a member of another group. From facts such as these I have tried to assess in what conditions each group would be most likely to thrive at the expense of other groups, and, conversely, what conditions would be sufficiently unfavourable to divide it into isolated populations from which the species developed. In postulating in each group successive climatic changes to account for the isolating and rejoining of the various populations I have been guided solely by the pattern presented by the birds themselves, and not by any consideration of what climatic changes are known from other evidence to have occurred, except that I have not, I hope, postulated any changes which are, on this evidence, outside the bounds of possibility. However, in the final section of the paper I have tentatively tried to correlate some of the climatic eras postulated with those known, as listed in Appendix 1.

In the discussion on evolution two assumptions are frequently made which are not necessarily correct but which seem sufficiently probable to justify their use as a basis for hypothesis. The first is the premise that the degree of divergence shown by two isolated forms can be correlated with the length of isolation. This, of course, is not necessarily true, but it can, I think, be accepted that in similar circumstance there is a likelihood that speciation will proceed at approximately the same pace; also that a comparatively long interval must elapse for considerable divergence to take place in isolates. The corollary premise that isolates that have not diverged extensively have not been long separated is more open to doubt, and examples (such as the forest owl *Phodilus prigoginei*) can be quoted of populations that must

have been long isolated but show little divergence. But I regard these as exceptional.

The second assumption is that the present species and potential species originated in some part or parts of their present range. This is a premise that is the more questionable in the case of species which are not members of superspecies. However, in the francolins these are exceptional, most of the species being part of a superspecies in which all members are allopatric and which has a more or less continuous distribution over a large part of Africa. In these cases it is highly improbable that the origin of any member was in the territory of the present neighbouring forms, although all may have been outside the present range of the group (i.e. when vegetation belts were pushed north or south).

In such a contingency each proto-species may be presumed to have held approximately the same position in regard to its neighbours as it does at present.

CHARACTERS

The study of the francolins in species groups has served to demonstrate that many characters which might be considered as guides to relationship show variable degrees of uniformity in each group. For example, in the Bare-throated Group the extent of bare skin on the face and throat is absolutely constant, and can be regarded as a "group character", whereas in other groups closely related species may have a variable amount of bare skin. It seems useful therefore to discuss some of these characters separately at the start in order to obtain an understanding of their importance. A summary of some of these characters is set out in Table 1.

SIZE

Little emphasis has been put on size or proportions in this paper, for though there is considerable individual variation there is reasonable uniformity in most related species. In the Red-winged Group the long-billed and short-billed populations of *F. shelleyi* provide the only example of marked proportional variation. On the whole general variation in size follows Bergmann's Law in relation to altitude and latitude, equatorial and lowland birds usually being smaller, but there are several inconsistencies. It is perhaps worth noting especially the incidence (for which I cannot account) of exceptionally small birds on the coasts of Kenya and southern Angola, and, to a lesser extent, Natal, since this feature is found in other genera besides francolins.

PLUMAGE

(a) *Feather patterns.* The complexity of the feather patterns has already been referred to. A number of examples are illustrated below which serve to define some of the descriptive terms I have used, and which have been arranged in sequences to indicate some of the transitional stages between one pattern and another. This is a subject which deserves fuller treatment than I can give it here and much of the discussion by Harrison in his paper "The incidence and origin of spotted patterns in the Estrildidae" (awaiting publication in the Ibis) is relevant to the francolins. It is sufficient here to emphasise that comparatively small changes in feather pattern,

SUMMARY OF SOME IMPORTANT CHARACTERS—TABLE 1

NOTES AND ABBREVIATIONS.

Column 1, *Size*. L—large, ♂ wing over 180 mm.; M—medium, 150–180 mm.; S—small, under 150 mm.

Column 2, *Sexual Dimorphism*. Species in which there is only a tendency for females to be more vermiculated are not shown as sexually dimorphic.

Column 3, *Bill*. u.m.—upper mandible; l.m.—lower mandible.

Column 5, *Normal Complement of Spurs*. Whole numbers indicate fully developed, sharp spurs; fractions indicate partly developed blunt spurs; "U" indicates an undeveloped spur evident as a swelling. When two spurs are present the lower is the longer unless otherwise stated. Numbers in brackets indicate that only a few sexed specimens have been examined.

Column 6, *Bare Skin*. Very small coloured patches behind the eye, or areas of dull bare skin are not shown.

Group	Species	1 Size	2 Sexual Dimorphism	3 Bill	4 Legs	5 Normal Complement of Spurs	6 Bare Skin
SPOTTED	<i>francolinus</i>	M-L	yes	black/brown.	red/orange-brown	♂ $\frac{1}{2}$, ♀o	
	<i>pintadeanus</i>	M	yes	black/brown.	orange/yellow	♂1 small, ♀o	
	<i>pictus</i>	S-M	slight	black/brown.	orange/yellow	♂o	
BARE-THROATED	<i>leucoscepus</i>	L	no	black, red base.	black	♂ $\frac{1}{2}$, ♀o	throat yellow, patch round eye, red.
	<i>rufipictus</i>	L	no	coral red.	brown	♂ $\frac{1}{2}$, ♀o	throat and patch round eye, coral red.
	<i>swainsonii</i>	L	no	u.m. blackish. l.m. dull orange.	blackish	♂1, ♀o	throat and patch round eye, red.
	<i>afra</i>	M-L	no	red.	red	♂ $\frac{1}{2}$ -1 $\frac{1}{2}$, ♀o	throat and patch round eye, red.
MONTANE	<i>erckelii</i>	L	no	black.	yellowish	♂2 (upper longest), ♀o	
	<i>ochropectus</i>	L	no	u.m. black, l.m. yellowish.	yellowish	♂2 (upper longest), ♀o	
	<i>castaneicollis</i>	L	no	red.	red	♂2 equal, ♀o	
	<i>jacksoni</i>	L	no	red.	red	♂ $\frac{1}{2}$, ♀o	eyelids, red.
	<i>nobilis</i>	L	no	red.	red	♂ $\frac{1}{2}$, ♀o	patch round eye, red.
	<i>cameronensis</i>	M-L	yes	orange-red.	orange-red	♂ $\frac{1}{2}$, ♀o	patch round eye, red.
SCALY	<i>swierstrai</i>	M-L	yes	orange-red.	red	♂ $\frac{1}{2}$ -1 $\frac{1}{2}$ (♀o)	
	<i>ahantensis</i>	M-L	no	orange, black base.	orange	♂ $\frac{1}{2}$, ♀o	
	<i>squamatus</i>	M-L	no	orange-red, dark culmen.	orange-red	♂ $\frac{1}{2}$, ♀o	
	<i>griseostriatus</i>	M	no	u.m. blackish, red base, l.m. orange-red.	orange-red	(♂1), (♀o)	

Group	Species	1	2	3	4	5	6
		Size	Sexual Dimorphism	Bill	Legs	Normal Complement of Spurs	Bare Skin
VERMICULATED	<i>bicalcaratus</i>	M-L	no	greenish, black culmen.	greenish	♂1½, ♀0	small patch round eye, yellow. small patch round eye, red.
	<i>icterorhynchus</i>	M-L	no	orange, black culmen.	orange	♂1½, ♀0	
	<i>clappertoni</i>	M-L	no	black, red base.	reddish	♂1½, ♀0	
	<i>hildebrandii</i>	M-L	yes	reddish, black culmen.	red	♂1½, ♀1-1½	
	<i>natalensis</i>	M-L	no (<i>natalensis</i>) slight (<i>neavei</i>) yes	reddish brown.	dull red	♂1, ♀0	eyering, yellow. round eye, red.
	<i>hartlaubi</i>	S-M	yes	u.m. horn, l.m. yellowish.	yellow	♂2U, ♀1-2U	
	<i>adpersus</i>	M-L	no	orange-red.	orange-red	♂1, ♀0	
	<i>capensis</i>	L	no	u.m. brown, l.m. reddish.	orange-red	(♂1½), (♀½-1)	
	<i>harwoodi</i>	L	?	red.	red	(♂1½)	
	<i>sephaena</i>	S-M	slight	black.	dull red	♂1, ♀0	
RED-WINGED	<i>streptophorus</i>	M	no	u.m. black, l.m. yellowish.	dull yellow	♂1U	
	<i>psilolaemus</i>	M-L	no	blackish.	dull yellow	♂1, ♀0	
	<i>shellei</i>	M	no	blackish, yellowish. at base.	dull yellow	♂1, ♀0	
	<i>africanus</i>	M	no	blackish brown.	dull yellow	♂1 small, ♀0	
	<i>levaillantoides</i>	M	no	blackish brown, yellowish at base.	dull yellow	♂1 small, ♀0	(♂1 small) (♀½)
	<i>levaillantii</i>	M	no	blackish brown, yellowish at base.	dull yellow	♂½-1	
	<i>finschi</i>	M-L	no	blackish.	yellow	(♂1 small) (♀½)	
	<i>coqui</i>	S-M	yes	black, yellow base.	yellow	♂1, ♀0	
UNGROUPED	<i>schlegelii</i>	S-M	yes	black, yellow base.	yellow	♂1, ♀0	patch, round eye, crimson. eyelids, green.
	<i>albogularis</i>	S-M	yes	black, yellow base.	yellow	♂1, ♀0	
	<i>lathamii</i>	S	yes	black.	yellow	♂1	
	<i>nahani</i>	S	no	crimson, black tip.	crimson	♂ none	
	<i>gularis</i>	M-L	no	black.	orange	♂1	
	<i>pondicerianus</i>	S-M	no	brown.	dull red	♂1	

particularly at the tip of the feathers, may greatly alter the appearance of a bird. (Compare the great differences in the general appearance of the breasts of a female *schlegelii* and a male *coqui*, and in the underparts of a male and female *pintadeanus* with the small differences in feathers 2 and 1, and 5 and 3 of Figure 1.)

(b) *Underparts*. The greatest variety of colour and pattern throughout the genus is found on the underparts (and to a lesser degree on the mantle) and considerable variation is found between closely related birds. The most striking example is illustrated by Bowen (1930) and shows the difference between the subspecies of

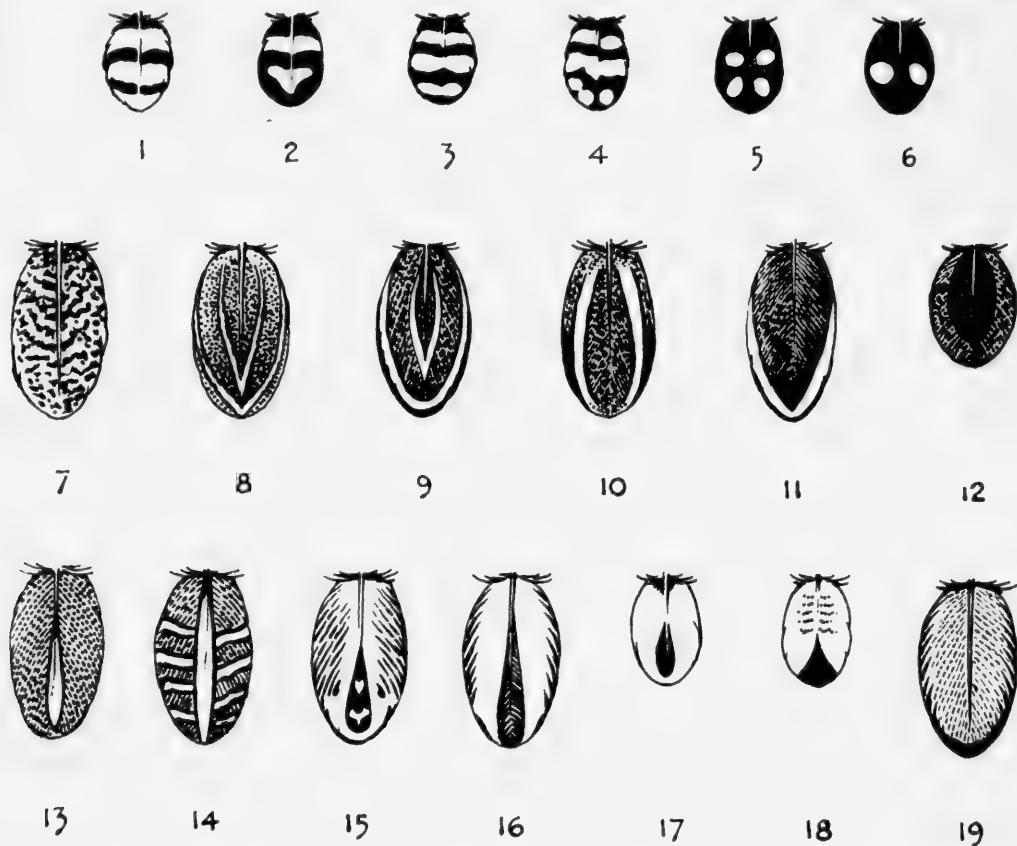


Fig. 1. Feather patterns.

1. Barred (*♂ coqui*, breast). 2. Barred with inverted triangle at tip (*♀ schlegelii*, breast). 3. Transition, barred to spotted (*♀ pintadeanus*, breast). 4. Transition, barred to spotted (*♂ shelleyi*, breast). 5. Transition, barred to spotted (*♂ pintadeanus*, breast). 6. Spotted (*♂ francolinus*). 7. Vermiculated (*hildebrandti*, back). 8. Irregular double-V-pattern (*harwoodi*, back). 9. Double-U-pattern (*clappertoni*, back). 10. U-pattern (*clappertoni*, back). 11. V-pattern (*clappertoni*, back). 12. Scalloped (*camerunensis*, back). 13. Striated (*sephaena*, back). 14. Quail-patterned (*shelleyi*, back). 15. Drop-shaped pattern with windows (*bicalcaratus*, breast). 16. Streaked (*jacksoni*, breast). 17. Drop-shaped pattern (*clappertoni*, breast). 18. Triangular pattern at tip (*sephaena*, breast). 19. Scaly (*squamatus*, breast).

F. afer with vermiculated underparts which hybridise freely with those with streaked underparts.

(c) *Upperparts*. The upperparts are basically either plain, streaked, vermiculated or "quail-patterned" (Fig. 1, 14), sometimes with a more complicated mantle patterning. While related species may vary between plain, streaked and vermiculated (see Montane Group) "quail-patterning" is more constant throughout the three groups in which it is found.

(d) *Wings and Tail*. The wings and tail are, on the whole, not conspicuously patterned or coloured, exceptions being found in the red wings of the Red-winged Group and some of the Red-tailed Group, and in the tails of the Red-tailed and Striated Groups which are reddish and black respectively.

A further exception is the light wing patch under the wing of *leucoscepus*, and rather similar light colour in the wings of *clappertoni*, which are the only members of their respective groups to have this character. These patches may have functional significance, for Harrison tells me he has observed the bare-throated *leucoscepus* in the London Zoo displaying with its wings carried forward exposing the light patch. Since other bare-throated francolins have plain wings it would be interesting to know if they have a different display, and also whether *clappertoni* and red-winged birds display in the same way.

(e) *Facial pattern*. Facial pattern seems to be an important character since it is the only feature of adult plumage which is recognisable in the chicks (see below), yet again related species show no constancy. In the Spotted Group two members have conspicuous facial patterns but *pictus* is unpatterned (yet hybridises with *francolinus*): in the Red-tailed Group the male *coqui* is unpatterned but the female patterned, the two sexes being recognisable in the chicks: in the Red-winged Group *finschi* is unpatterned but all other members have a black bridle and necklace, either well defined or indicated by spotting. Unfortunately chicks of many of the critical species are not available.

It has proved impossible to include a summary of plumage in Table 1, since the variation in colour and pattern is too complex to put into a few words. In the text I have tried to give sufficient descriptions to enable the reader to form a picture of the bird but without going into full detail.

SEXUAL DIMORPHISM

As a rule in francolins the sexes are alike except that the male is more heavily spurred and the female often slightly more vermiculated, but there is marked sexual dimorphism in all members of the Red-tailed Group: in two out of nine members of the Vermiculated Group, one of which hybridises, and in part intergrades, with another member in which the sexes are alike: in two out of three members of the Spotted Group: in two out of seven members of the Montane Group, and in *lathamii*.

EXTENT OF BARE SKIN

Bare skin on the throat as well as round the eye is found only in members of the Bare-throated Group (though not in the chicks). Various other species scattered

through different groups have conspicuous bare patches round the eye, namely *camerunensis* and *nobilis* in the Montane Group, *harwoodi* in the Vermiculated Group, and *nahani*. Others have smaller patches (*clappertoni*, *icterorhynchus*, and *adpersus* in the Vermiculated Group)—or coloured eyelids (the montane *jacksoni*)—or small coloured patches behind the eye. Unfortunately these smaller patches have largely been ignored by collectors especially when they are not brightly coloured and it is difficult to ascertain from skins in which species they are present, or if colouring is seasonal: to avoid error only conspicuous areas of coloured skin are therefore mentioned in the table.

COLOUR OF BILL AND LEGS

This is a character that is reasonably constant in half the groups but very variable in the others, striking variation being found between the three northern species in the Vermiculated Group which otherwise form a remarkably homogeneous assemblage.

SPURS

The number of spurs carried by males and females in any species is not constant, and indeed has been known to differ on the two legs, nevertheless there is sufficient constancy to justify the term "normal complement". This varies between species, from a complete lack of spurs in either sex in *pictus* of the Spotted Group and *nahani* to two fully developed spurs in the males of *erckelii* in the Montane Group. Blunt, half-developed spurs are found even in adult birds, often in males as an upper spur, and occasionally in females of almost all species that are normally without spurs. In the rare cases where a bird has a normal complement of two fully developed spurs it seems that the upper is likely to be equal to or longer than the lower, but in the cases where a bird has one fully developed and one half-developed spur it is the lower which is fully developed and therefore the longer. Undeveloped spurs are indicated by swellings and are found normally in fully adult males of the vermiculated *hartlaubi*, and the striated *streptophorus*. It can be said, therefore, that the number of spurs has some taxonomic significance, but is not as infallible or as important a character as some text books lead students to believe.

FIELD HABITS

I have too little personal experience of francolins in the field and too little has been written, especially of some of the rarer species, for me to make much use of habits and behaviour as criteria of relationship. There is a certain amount of information on whether or not the birds are found in coveys, and whether they perch or roost in trees, but no one group is fully documented. It can be said confidently, however, that the majority of francolins are found in pairs or small coveys according to the season, but four species at least are more gregarious: in the Vermiculated Group *bicalcaratus* is found in coveys of up to 40 birds (Bannerman, 1930: 321), and *adpersus* up to 20 (McLachlan & Liversedge, 1957: 96); and in the Red-winged Group *africanus* is found in coveys up to 30 birds (Horsburgh, 1912: 47), and

levaillantoides up to 14 (op.cit.: 54). I have found definite records of most members of the first five groups taking to trees though they do not necessarily use them regularly for roosting: Hopkinson (1923: 128) found *bicalcaratus* roosted in trees only in the rains, and this may well be true of other species. On the other hand I have no records of any members of the last three groups, the Striated, Red-winged and Red-tailed, taking to trees even when alarmed and it would seem that these birds, with their more cryptic ("quail-patterned") coloration rely for protection on sitting close.

HABITAT

It will be shown in the discussion on the groups that the majority of the francolins have very precise ecological requirements, so much so that, though several different species may be found in the same area, it is rare to find two different species on the same ground. For instance at Onguati in South West Africa *F. adspersus*, *F. levaillantoides* and *F. hartlaubi* were found within a few hundred yards of each other, but *adspersus* was strictly confined to the riverine vegetation, *hartlaubi* to the rocky kopjes and *levaillantoides* to the grasslands between (Macdonald, 1957: 52). Similar instances are found throughout southern and eastern Africa where the ranges of six groups overlap but there are also exceptions. Pitman has found *coqui*, *levaillantii* and *afer* on the same ground in Uganda: Elliot also has found *coqui* with other species in Tanganyika and Blasdale has found it with *bicalcaratus* in Nigeria (but not with *clappertoni*): Benson and Stuart-Irwin have found *natalensis* and *sephaena* together in riverine thickets in both Northern and Southern Rhodesia, and Stuart-Irwin tells me that *sephaena* is also found with *adspersus* in Ngamiland, though in Southern Rhodesia the two would never occur together: *adspersus* also occurs with *swainsonii*, sometimes in the same flocks, in Ngamiland. All these examples are of members of different groups occurring together but hybrid specimens show that members of the same group may mix where they have a common boundary, as indeed would be expected.

In any one group the different species may all share the same, or very similar, ecological preferences, as in the Spotted and Scaly Groups, or different species may have different preferences, as for example in the Red-tailed and Bare-throated Groups. There are also individual species which show a wide choice of habitat in different parts of the range, most notably the red-winged *F. shelleyi* and the red-tailed *F. coqui*, and similar inconsistency is shown in the altitude at which some species are found, especially among all members of the Red-winged Group (except the Montane Redwing, *F. psilolaemus*) and in *F. squamatus* of the Scaly Group.

VOICE

It would seem that voice should be a guide to relationship in the francolins but the few direct comparisons that have been made between species indicate that there are unexpected inconsistencies and affinities. Benson, for instance, records a remarkable difference in the call of *sephaena* in Abyssinia and Rhodesia (1958: 191), yet considerable uniformity in both *levaillantii* and *coqui* between the calls of north

and central African birds (1948: 52). He tells me also that there is a marked family resemblance in the voice of three members of the Red-winged Group, *levaillantii*, *shelleyi* and the Abyssinian *levaillantoides*, and in three members of the Bare-throated Group, *afer*, *swainsonii* and *leucoscepus*. Similarities between members of the Montane and Scaly Groups respectively have been recorded by Hall (1960a: 408) and Collier (1935: 666). Furthermore Chapin (1932: 715) found the call of the bare-throated *afer* indistinguishable from that of *icterorhynchus* of the Vermiculated Group. On the other hand Blasdale tells me that the red-tailed *coqui* and *albugularis* in Nigeria have quite different calls.

CHICKS

I have only been able to examine chicks of less than half the species and it is only possible therefore to draw a few general conclusions. The most striking variation is shown in the pattern of the crown and face, but in this respect there is little difference between the representatives examined of the Bare-throated, Montane, Scaly or Vermiculated Groups, all of which have a solid brown crown (sometimes edged black) and a single conspicuous brown or blackish stripe from the bill through the eye to the neck. In addition the only chick examined of the Montane Group (*erckelii*) has a short black stripe below the eye. The chicks of the Red-winged Group are distinctive in having a narrow and darker crown patch, bordered on each side by eight alternate white and black stripes over, through and under the eye, the forerunner of the adult bridle and necklace. Unfortunately no chick has been examined of *F. finschi*, the only member of the group without any black-and-white bridle or necklace, and none of *F. psilolaemus* in which the bridle is spotted and indistinct. The female *coqui* of the Red-tailed Group has a similar pattern to the red-winged chicks though less clearly defined, but the male chick is like those of the other groups, though with the brown of the crown extending further forward to the beak: the chicks therefore bring out the sexual dimorphism of the adults. The adults of the Spotted Group have, like those of the Red-winged Group, a very striking facial pattern, and the chicks have a similar narrow crown patch with alternate stripes on either side, but the pattern is paler than in the Red-wings and ill-defined. The chick of the ungrouped *pondicerianus* has an indefinite pattern intermediate between both main varieties, the dark stripes above the eye being incomplete and ill-defined. In view of the small variation evident between the chicks of many species and even groups, it is interesting to note that subspecific variation is apparent between the paler and darker races of *F. francolinus*, and between two "potential species" of the Red-winged Group *F. s. shelleyi* and *F. s. whytei*.

EGGS

The British Museum has a reasonably representative collection of francolin eggs, including those of at least one member of every group, but as a guide to relationship they are disappointing. All are rather broad, and are plain or lightly freckled, ranging in colour from white to light brown. Large series of eggs of both *F.*

bicalcaratus and *F. francolinus* show there is considerable variation in colour within a species, largely correlated with the darker and paler subspecies living in wetter or drier conditions. There is also some variation in shape. The eggs of the two African forest francolins *lathamii* and *nahani* are the most distinctive, those of *lathamii* (represented by two clutches from the Cameroons) being a plain reddish brown and more elongated than any others, and those of *nahani* (represented by one clutch from Uganda) being the most heavily freckled, brown on a buff ground. Pitman tells me that the eggs of *sephaena* are also distinctive in having an exceptionally hard shell.

THE SPOTTED GROUP (MAP 1) (*F. francolinus*, *F. pictus*, *F. pintadeanus*)

RANGE AND CHARACTERS

The Spotted Group is the only Asiatic group and is formed by three of the five Asiatic species. It ranges from south China and the Indo-Chinese countries through Thailand, Burma, the Indian sub-continent, Ceylon, Persia, Iraq to the eastern Mediterranean and Cyprus. There is evidence that it has also inhabited many of the Mediterranean countries and islands in historical times (Lilford, 1862, Lavauden, 1936). Its members are birds of grassland and scrub jungle, and are found also in cultivations where there is sufficient cover. They occur up to 5,000 ft. but commonly prefer lower altitudes.

They are mostly medium-sized, with the mantle either spotted or V-patterned in brown and buff and the back and tail narrowly barred in black and white, or buff and brown: the wings are barred or spotted. Below they are basically black or dark brown with white spots, but in the females of two of the species (*F. francolinus* and *F. pintadeanus*) these spots are merged together and elongated to form irregular bars. The under tailcoverts are maroon. The bills are black or dark brown and the legs vary from yellow to red-brown. Spurs are poorly developed, the normal complement for the males of *F. francolinus* and *F. pintadeanus* being one only, and that rather short and blunt, while *F. pictus* is without spurs in either sex.

SPECIES AND POTENTIAL SPECIES

The three recognised species are the only mainland forms with which we need be concerned for other variation is clinal and ecological and does not suggest that any smaller populations have been isolated for any length of time from the main body. The species are quite distinct: the western *F. francolinus* has marked sexual dimorphism, the male having the throat, breast and sides of face largely black, with sparse white spots on the side of the breast, and white cheeks: it has a complete broad maroon collar and some black feathers with white spots on the upper mantle; the rest of the mantle and wing coverts are V-patterned in buff, brown and occasionally black.

The female has no black, the throat being whitish, the sides of the face mottled brown and buff, and the underparts irregularly barred in brown and off-white.

The upperparts are patterned like those of the male but without black and with the maroon collar replaced by a small rufous patch on the hind neck.

The range of *F. francolinus* extends eastwards to Manipur. It is replaced in southern India by *F. pictus*, a smaller bird with little sexual dimorphism, but in females there is a tendency for the patterning on the abdomen to merge into bars and this seems most pronounced and most constant in the Ceylon population (*watsoni*). The face and throat of *F. pictus* are unpatterned and rich ochre in colour: the upperparts are similar to those of the female *F. francolinus* but with more spotting in the mantle and no rufous collar patch: the underparts are intermediate between the male and female of *francolinus* being basically black, or very dark brown, regularly covered all over with large buff spots.

Where the ranges of the *F. francolinus* and *F. pictus* meet in Rajasthan (Rajputana), Uttar Pradesh (United Provinces) and Bihar there is no natural barrier between them, and no ecological distinctions have been noted. It is evident that they do not interbreed freely but do so occasionally for there are four specimens in the British Museum which appear to be hybrids: these are from Deesa (the type of *F. intermedius*), "Neemsar" (an unplaced locality probably, from the history of the collector, near Fateghur) and "Bihar" (no detailed locality).

Ceylon birds are not very different from those of the mainland, but are rather darker and more closely patterned, with the tendency (already noted) for the females to be slightly barred on the abdomens.

East of Manipur *F. francolinus* is replaced by *F. pintadeanus* which, in both sexes, differs from the other two species in having the throat and cheeks white, sharply divided by a black line, and having the mantle largely spotted, not V-patterned, and with a considerable amount of rufous, especially in the male. Below the male is patterned all over like *F. pictus*, but with the spots pure white on a deep black ground; the female is barred like the female of *F. francolinus* but with the barring narrower and more sharply contrasted.

The higher ranges of Manipur and the Chin Hills seem to form an effective barrier along most of the boundary between *F. pintadeanus* and *F. francolinus* though they might be expected to meet along the coastal strip. I know of no records of hybridisation between them.

OTHER VARIATION

Variation is clinal. In *F. francolinus* western birds are large and dark (*francolinus*), grading through *arabistanicus* of Persia and Iraq to the small, pale, grey birds of Baluchistan and western India (*henrici*). Birds of north-eastern India are darker again (*asiae*) grading into the very dark *melanotus* of Assam.

In *F. pictus* there is a pale population in the drier north-western areas (*pallidus*) and other mainland birds (*pictus*) are intermediate between *pallidus* and the darker Ceylon birds (*watsoni*).

In *F. pintadeanus* birds from southern China and northern Indo-China are paler, less heavily patterned than those of Burma and Thailand (*phayrei*).

EVOLUTION

The Spotted Group presents a straightforward pattern of three allopatric species with a continuous distribution across sub-tropical Asia. To interpret this pattern

it is only necessary to visualise less favourable conditions in the northern parts of the present range which would serve to isolate the three species from each other.

I suggest therefore that the three species have arisen from a single species occupying the present range of the whole group, and possibly much of southern Europe as well. In an unfavourable era, such as a Glaciation, conditions in the northern parts of the range became unsuitable and *proto-francolinus* was isolated in Palestine and possibly Arabia (if the era was wet as well as cold): *proto-pictus* was isolated in southern India and *proto-pintadeanus* was isolated in south-eastern Asia (Map 1A). With the return of favourable conditions the three species spread north again, *proto-francolinus* invading India from the west and establishing itself north of *proto-pictus*. In the period of isolation speciation had developed sufficiently for the three species not to interbreed freely when they rejoined, but the presence of hybrids on the boundary between *francolinus* and *pictus* indicates that genetic isolation is not absolute.

A summary of the evolution postulated is, therefore, as follows:—

Stage 1. The ancestral form of the group widespread, covering present range and possibly southern Europe as well.

Stage 2. An unfavourable era, probably a Glaciation, pushes the range southwards isolating the ancestral stock of the three species in south-western Asia, southern India, and south-eastern Asia (Map 1A).

Stage 3. With the return of more favourable conditions the group spreads northwards again, but speciation had advanced sufficiently in the three isolated blocks to inhibit free interbreeding when they rejoin.

THE BARE-THROATED GROUP (MAP 2)

(*F. afer*, *F. swainsonii*, *F. rufopictus*, *F. leucoscepus*)

RANGE AND CHARACTERS

The Bare-throated Francolins are widespread in eastern Africa from Eritrea to Cape Province and westwards, south of the Congo forest, to Gabon, Angola and northern South West Africa. They are found at comparatively low altitudes, usually near water-courses or in grasslands with cover of trees and scrub in which to hide.

They are large francolins distinguished by having a conspicuous patch of bare skin on the throat and round the eye, varying in colour from scarlet to yellow. The bill and legs vary from red to black (never yellow): spurs are fairly well developed, the males of all species having normally a long and strong lower spur; a short blunt upper spur is found commonly in two of the species (*F. leucoscepus* and *rufopictus*), less often in *F. afer* and rarely in *F. swainsonii*. In the group as a whole the upper parts are plain brown from the crown to the tail, with some darker centres to the feathers of the mantle and a few light vermiculations, but in one species (*leucoscepus*), the mantle feathers have white shaft streaks, and in another (*rufopictus*) they have broad rufous edges. The underparts are, on the whole, streaked, but vary widely in colour and in the amount of vermiculation. The sexes are alike except that the females tend to be slightly more vermiculated.

SPECIES AND POTENTIAL SPECIES

The Bare-throated Group is a far more complicated assemblage of forms than the distribution of the four species suggests, for variation in colour and pattern among the populations of *F. afer* shows it has had a turbulent history and that at some time at least six of its subspecies have been isolated for a sufficient period for them to have diverged considerably.

The species themselves are largely allopatric and ecologically segregated, overlapping only in a few marginal areas. The most distinctive member of the group (*F. leucoscepus*) is confined to the acacia steppe of the north-east (Map 11, Type 25). In *leucoscepus* the bare skin is red round the eye, yellow on the throat, the bill black with a red base and the legs black: the mantle has white shaft-streaks and the underparts are irregularly streaked all over with plain brown and white, each feather being brown with narrow white edges and a triangular white patch at the tip, tapering up the shaft: there is a faint rufous tinge in the brown parts of many feathers. The primaries have some white on the inner wings which forms a conspicuous patch when the wing is displayed: there is no comparable patch in other members of the group.

F. leucoscepus is replaced by another species, *F. rufopictus*, in a small area of Tanganyika stretching from the south-eastern shore of Lake Victoria to the Wembere.¹ This area is still within the dry belt of acacia steppe but differs from typical *leucoscepus* country in the types of *Acacia* species present (*Stronach in litt.*), so it may possibly form an ecological island particularly suited to *rufopictus*.

In *rufopictus* the bare skin is coral red, the bill is red and the legs brown: the feathers of the upperparts are basically grey-brown with dark vermiculations and dark shaft-streaks, with the feathers of the mantle and wing coverts broadly edged with chestnut: the breast is mainly grey with black shaft-streaks and the rest of the upperparts streaked black, white and chestnut; the eye-stripe and sides of the face are black and white.

In southern Africa there is a third species (*F. swainsonii*) associated chiefly with acacia country, ranging in the acacia/mopane savanna belt (Map 11, Types 20 and 22) from South West Africa to Mozambique and extending up the Loangwa valley to the Nyasaland border. In Southern Rhodesia, however, it is found scattered through the grasslands of the woodland belt, eastwards to the Mashonaland plateau.

In *F. swainsonii* the bare skin is red, the bill black above and orange below, the legs black, with the single spur in the males very long and strong: both above and below it is a pale brown with some darker shaft-streaks; it has a faint grey wash over the breast and chestnut streaking on the abdomen. Populations of the Transvaal and southern Southern Rhodesia (*F. s. swainsonii*) have a blackish mottled patch on the abdomen.

The fourth species, *F. afer*, inhabits rather wetter areas than the other three. Throughout central Africa its range coincides with the extent of the woodlands,

¹ I can find no confirmation, either from museums or from field workers, of the statement by Van Someren (1925: 99) that *F. rufopictus* occurs in Ruanda. No actual specimens or localities were quoted.

except in western Southern Rhodesia where these are occupied by *F. swainsonii* (see above), and in southern Angola where it has intruded into a small area of the acacia belt. In South Africa there are two isolated populations in the south-eastern Transvaal and in the coastal strip of southern Natal and Cape Province.

In *F. afer* the areas of bare skin, the bill and the legs are red: the back is plain brown with some darker feather centres. The sides of the face and the underparts show considerable variation and two diverse blocks of subspecies are easily recognised, separated by two areas of hybridisation. The first block comprises all the populations of the southern Congo, northern Angola, Northern Rhodesia east to the Muchinga Escarpment, extreme western Tanganyika, Uganda and the shores of Lake Victoria. These birds are heavily vermiculated on the underparts, with sparse chestnut streaks on the abdomen: the feathers of the face are minutely patterned in black and grey. I can recognise no significant geographical variation throughout this area and all populations may be referred to *F. a. cranchii*, except for some very dark birds in the Ruzizi valley, north of Lake Tanganyika (*harterti*) in which the streaks on the abdomen are maroon rather than chestnut; also the populations bordering on the hybrid zones in Northern Rhodesia and Tanganyika have a mixture of white in the abdomen (*F. a. intercedens*).

In the second block the birds have no vermiculation and are strongly patterned in black, white and grey on the face and underparts, and only the subspecies of south-eastern Cape Province has any chestnut or maroon. The black-and-white subspecies have a broken distribution, one, *F. a. afer*, being restricted to the south-western corner of Angola along the Escarpment and in the Cunene basin. In *F. a. afer* the face is white and the underparts broadly streaked in white and black, the feathers having black centres and white edges.

The rest of the block is found in the eastern half of the country and comprises an assemblage of subspecies north of the Limpopo and two isolated populations in South Africa. The northern birds all have the feathers of the breast grey with black shaft streaks contrasting with the feathers of the abdomen, which are mainly plain black, and those of the flanks which are streaked black and white. Birds of the coastal population of Kenya (*leucoparaeus*) have the eyestripe black and white and the sides of the face white. They are replaced in northern Tanganyika by birds with a wholly black face, and similar birds are found south to southern Nyasaland and extreme south-eastern Northern Rhodesia (*melanogaster* and *loangwae*). There is no information as to whether or not there is intergradation between *leucoparaeus* and *melanogaster* but birds typical of these forms are found within 110 miles of each other at Mombasa and Korogwe respectively.

Birds from the eastern districts of Southern Rhodesia and southern Portuguese East Africa have the whole face and a necklace above the breast white (*swynnertoni*). In the lower Zambezi valley, the Salisbury area of Southern Rhodesia, and in southern Nyasaland, between the ranges of the black-faced and white-faced forms, there is an unstable population with a variable amount of black and white in the face (*humboldtii*).

Birds of the isolated population in Natal and Cape Province are again differently patterned, having the face wholly black, and the underparts from the upper breast

to the abdomen streaked with white, maroon and black, the white lying in parallel streaks on either side of the shaft (*castaneiventer*). These birds intergrade in the region of Uitenhage with the populations of the southern Cape in which the maroon is wholly replaced with black (*notatus*).

In Natal Vincent tells me that *castaneiventer* is found only between 2,000 and 4,000 ft., usually on the edges of evergreen forest. It is absent from northern Natal and the coastal belt (where its place is possibly taken by *F. natalensis* of the Vermiculated Group). There is, however, an isolated population in the south-western Transvaal (*lehmanni*) which is intermediate in some respects between the *castaneiventer/notatus* forms and *swynnertoni*, having the face black and the abdomen with long parallel white streaks as in *notatus*, but the whole breast grey, with black shaft streaks, contrasting with the abdomen as in *swynnertoni*.

Between the block of vermiculated and chestnut forms in the north and the blocks of black-and-white forms in the east and in southern Angola there are two hybrid zones, one stretching from Kondoa and Dodoma in central Tanganyika through central Nyasaland into the Luangwa valley, the other through northern and central Angola into extreme north-western Rhodesia. The hybrid populations of Tanganyika and Nyasaland have well-defined streaks on the abdomen varying in the proportion of chestnut to black-and-white according to the proximity of the respective parent forms, but most birds from the same area are reasonably constant and can be distinguished from birds of other local populations. This does not seem to be true in Angola where micro-populations show greater variability, and the streaking on the abdomen is less regular and less defined.

In Kenya and Tanganyika *F. afer* replaces *F. rufopictus* and *F. leucoscepus* without apparently any overlap, but its relations with *F. swainsonii* in southern Africa vary. In the Luangwa valley, where both occur, *F. afer* is found chiefly in the riverine vegetation and *F. swainsonii* in the acacia and mopane (Benson and White, 1957: 23) and the same applies in the Namwala, Mumbwa and Lusaka districts (Benson). The same is probably true in the Zambezi and Limpopo valleys. However, in Southern Rhodesia where *F. swainsonii* has intruded into the woodland belt the two come together without any ecological segregation, so that both occur on the same ground.¹ In this area two birds have been collected which show characters of both species, one from near Salisbury (the type of *Pternistis cooperi*, Roberts, 1947) and the second from Hartley's Farm, Rusape, where both species are found (Smithers, *in litt.*). Other specimens of *F. afer* from the same farm have been noted to have dark brown instead of the normal red legs. This suggests strongly that some hybridisation takes place along this border.

There is a record of a third specimen which shows characters of both species (Markus, 1959), but this was collected at Francistown, three hundred miles from the nearest race of *F. afer*, or from any suitable habitat. It was unfortunately not preserved, but Markus (*in litt.*) described it as having a red bill and legs, no white on the face, but both white and chestnut markings on the abdomen, the white markings being like those of *F. a. lehmanni* and the chestnut like those of *F. swainsonii*.

¹ Smithers tells me that, with the clearing of land for farming, *F. swainsonii* has entirely replaced *F. afer* in parts of the Salisbury area within the last fifty years.

Since it is unlikely that there is an isolated population of *F. afer* in country that is both unsuitable and reasonably well known ornithologically, it must be regarded as an aberrant specimen of *F. swainsonii*, emphasising the close relationship of *afer* and *swainsonii*.

The exact ranges of *F. afer* and *F. swainsonii* in southern Angola are not known, nor is there any information on their relationship.

OTHER VARIATION

In *F. leucoscepus* variation is slight. Birds of the coastal areas of Eritrea and western Somaliland (*F. l. leucoscepus*) have rather more white on the feathers of the underparts than birds from other parts of the range (*F. l. infuscatus*), but elsewhere variation in the general darkness or paleness and degree of patterning of populations is sporadic in local populations.

Apart from the dark birds of the Transvaal and southern Southern Rhodesia (*F. s. swainsonii*) which have a mottled black patch on the abdomen, the variation in this species is linked with ecology. Eastern birds (*lundazi* White, 1947) are rather browner, less grey than those of the semi-desert areas of northern Bechuanaland and northern South West Africa (*gilli*) while another rather browner population may be recognisable from the Waterburg area (*damarensis*). (Hall, 1956: 100, Benson & White, 1957: 23, 138). Southern birds average larger.

In the stable populations of *F. afer* there is little variation that has not yet been discussed, but in the black-bellied, black-faced populations there is some clinal variation, birds of Tanganyika (*melanogaster*) being paler and less brown than those of Nyasaland and Northern Rhodesia (*loangwae* Grant & Praed, 1934).

EVOLUTION

The pattern presented by the Bare-throated Group is complex, for not only is there evidence of considerable hybridisation taking place at present but the morphological characters of the different species, and the degree and type of variation among the subspecies, suggest incidences of past hybridisation as well. A simple sequence of evolutionary stages is therefore difficult to envisage and it is perhaps best to start by discussing the features of the pattern that can be readily interpreted. It is apparent, for instance, that the present is a favourable era for *F. afer* since the hybrid zones indicate that it now occupies areas from which it has recently been absent. The diverse characters of the *afer* subspecies point to a lengthy period in which the two blocks of vermiculated and black-and-white subspecies were isolated from each other. Since neither apparently developed ecological preferences in that period they were able to interbreed when the ranges rejoined. Similarly the variation between many of the black-and-white populations points to periods in which they have been isolated.

Comparison between Map 2 and the vegetation map shows that the ends of the hybrid corridor through the Luangwa valley and central Tanganyika coincide with the intrusive tongues of acacia into the woodland belt. This suggests that the two *afer* blocks were divided from each other in a dry era when this corridor was wholly covered by acacia and occupied by the acacia species. It seems probable that dry conditions prevailed at the same time in most of Angola eliminating *afer* from the present hybrid zone and isolating the small population in the south in the region of the Angola escarpment where moister conditions might still be expected through proximity to the sea (see Hall, 1960). Similar dry conditions would serve also to split the eastern populations.

It is more difficult to visualise the conditions in which the four species were originally isolated from each other, and particularly so in the case of *afer* and *swainsonii*, which now occupy neighbouring vegetational zones with a common boundary of 10,000 miles. These two species seem to be the most closely related since they are alike above and in the colour of the bare skin; furthermore they apparently hybridise now in one limited area and the dark patch on the abdomen of *F. s. swainsonii* may be an indication of more extensive hybridisation in the past. They may therefore be assumed to have separated most recently. Conversely the distinctive *F. leucoscepus* was probably the first to be split from the ancestral stock of the group. *F. rufopictus* in some ways combines the characters of the other three species, having vermiculated, chestnut, white and black patterning in the feathers and having the bare skin orange, rather than yellow or red. It is possible that it may represent a relict population approximating more closely to the ancestral form of the whole group, or else be a product of past hybridisation between species that has become stabilised and established itself in an ecological island. Both these alternatives are very speculative and in selecting the latter as slightly more probable I have been guided by the resemblance of *rufopictus* on the underparts to some of the hybrids between the main blocks of *afer* subspecies. Its present distinctiveness and ability to live alongside both *leucoscepus* and *afer* without interbreeding suggest an early origin, probably before *afer* and *swainsonii* diverged.

I would postulate therefore that the bare-throated francolins were originally birds of acacia and that they were first split by a spread of woodland or forest into a north-eastern population (proto-*leucoscepus*) and a southern population (proto-*afer/swainsonii*). Later the two rejoined briefly and hybridised forming proto-*rufopictus*, a relict population which was left in Tanganyika in a subsequent wetter era when *leucoscepus* withdrew further north and proto-*afer/swainsonii* further south.

It is necessary now only to envisage some circumstances in which *afer* and *swainsonii* could develop. I can suggest no likely vegetational changes that would form a west-east barrier on similar lines to the present boundary, and conclude that they were split originally into an eastern population (proto-*afer*) and western population (proto-*swainsonii*) divided by a barrier of forest through Natal and the eastern districts of the Transvaal and Southern Rhodesia. In isolation proto-*afer* became adapted to wetter conditions and independent of acacia so that in a subsequent period was able to spread across to Angola through the woodland belt. It may have hybridised with *swainsonii* to a limited extent in the east but, for the most part, was ecologically segregated. It may also have hybridised to a limited extent with *rufopictus*, giving northern birds a higher proportion of chestnut and vermiculations in the feathers than the southern. (This is a possible way to account for the different directions in which the northern and southern blocks of *afer* diverged.) No subsequent changes affected the status of the four species and only *F. afer* was subject to further splitting and rejoining, though the ranges of the others would have spread and contracted in alternate dry and wet spells. It has already been suggested that a dry spell with a spread of acacia was responsible for isolating the two main blocks of *afer* subspecies and also the small population in southern

Angola. This diverged from the northern block along much the same lines as the southern block in the east, with black-and-white pattern predominating. Subsequently minor fluctuations would serve to isolate the various eastern populations of *afer* producing the subspecies *leucopareus*, *melanogaster*, *swynnertoni*, *castaneiventer* and *notatus*. In South Africa the population of the Transvaal (*lehmanni*), intermediate between *swynnertoni* and *castaneiventer*, may have once formed part of cline between them but has been isolated from both, possibly by the intrusion of *F. natalensis* of the Vermiculated Group.

A summary of the evolution postulated is therefore as follows:—

Stage 1. The group widespread in acacia.

Stage 2. The group split by a spread of forest, proto-*leucoscepus* isolated in the dry north-east, proto-*afer/swainsonii* in the south.

Stage 3. Less humid: the two populations rejoin briefly and hybridise producing proto-*rufopictus*. Proto-*afer/swainsonii* spreads across the southern part of the continent.

Stage 4. Proto-*swainsonii* in the west is separated from proto-*afer* in the east by a barrier of forest. In isolation proto-*afer* becomes adapted to wetter conditions (Map 2A).

Stage 5. Proto-*afer* spreads across to Angola through the woodland belt, possibly hybridising to a limited extent with both *swainsonii* in the south-east and *rufopictus* in the north.

Stage 6. In dry conditions *afer* is divided into two main blocks, one in the north and one in the south-east, with a small population isolated in southern Angola. In isolation the northern block develops distinctive chestnut and vermiculated patterning below, and the two southern populations a black-and-white patterning (Map 2B).

Stage 7. Minor fluctuations isolate the various eastern populations of *afer*.

Stage 8. A favourable era for the group as a whole and particularly for *afer*, the vermiculated and the black-and-white blocks of subspecies rejoining and interbreeding forming hybrid zones in the east and west. Among the eastern black-and-white subspecies the white-browed *swynnertoni* and the black-browed *melanogaster* meet and hybridise in the lower Zambezi valley.

THE MONTANE GROUP (MAP 3)

(*F. erckelii*, *F. ochropectus*, *F. castaneicollis*, *F. jacksoni*, *F. nobilis*, *F. camerunensis*,
F. swierstrai)

RANGE AND CHARACTERS

The Montane Group, as its name implies, is formed of scattered communities in the mountains of north-eastern Africa from Eritrea to Mount Kenya, on the eastern Congo border, in the highlands of Angola, and on Cameroon Mountain. Its members are birds which require some trees for cover and roosting and the majority of species are found in or near montane evergreen forest: only members of the northern species (*F. erckelii*) are less associated with forest being found on the grasslands of the high plateaux of northern Abyssinia where there are neighbouring woods.

In appearance this is the least homogeneous of the groups, so much so that it is

impossible to designate any "group" character other than that the males have the crown, lower back, primaries and tail plain brown or red-brown, and the females, in the species in which they are unlike the males, have the primaries, lower back and tail vermiculated. However, variation in the other characters seems to follow geographical trends, the birds of the extreme north-east being the largest and most heavily spurred with dark bills, yellowish legs, no bare skin round the eye and with the sexes alike, or only very slightly differentiated by a tendency for the females to have some vermiculations on the wing and tail. Birds of the two isolated western populations are the smallest, least heavily spurred with red bills and legs, and with the sexes quite unlike: in the Cameroon population there is an extensive area of red bare skin round the eye. The central species have some characters in common with one or both of their nearest neighbours so that all are linked. The variation in the colour and pattern of the underparts is considerable, but no more extreme than that found in one species (*F. afer*) of the Bare-throated Group. Taking these factors into account, together with the affinities of other birds and plants of the same montane communities, I am confident that it is correct to regard the montane francolins as a superspecies.

SPECIES AND POTENTIAL SPECIES

F. erckelii is the northern representative of the group and has a fairly continuous distribution in the grasslands of the Abyssinian massif from the Addis Ababa area northwards to southern Eritrea. An isolated population (*pentoni*) is found in the Red Sea Hills at Erkowit, which differs only in being rather greyer. *F. erckelii* is rarely found below 6,000 ft. and ranges up to 10,000 ft. It appears to be less dependent on the presence of evergreen forest than other members of the group, which would account for its more continuous distribution, and this continuity is reflected in the birds themselves, which are remarkably uniform in colour and pattern.

It is the largest of the francolins, with a black forehead and eyestripe, chestnut crown, the mantle and breast largely grey with maroon streaks and the rest of the underparts white with maroon streaks: the sexes are alike: the bill is black and the legs yellowish, the male having two spurs of which the upper is the longer.

On the Plateau du Day in (French) Somaliland there is an isolated population (*F. ochropectus*) living in the juniper forest above 3,500 ft. (Dorst & Jouanin, 1950). It is similar to *F. erckelii* in many respects of pattern but is dull in colour having the maroon and chestnut replaced by ochre or brown, and it has some U-patterning on the lower mantle: the bill is blackish with some yellow on the lower mandible: the legs are similar in colour and spurs to *F. erckelii*. It is in fact intermediate in many respects between *erckelii* and *F. castaneicollis* of southern Abyssinia but possibly sufficiently distinct from both to be granted specific rank.

The nearest population of *F. castaneicollis* is found within 150 miles of *F. ochropectus* in the mountains of western (British) Somaliland. Other populations are found in the massif of the Arussi plateau in Abyssinia east of the Rift, and in the montane "islands" over 6,000 ft. in southern and south-western Abyssinia.

It is apparently more dependent than *F. erckelii* on cover such as juniper and other evergreen forest and bamboo and, since forested patches over 6,000 ft. may be widely separated by unsuitable country, the range is very broken. In conditions such as these divergence between populations is to be expected and the species is, in fact, very variable, though individuals from the same populations are reasonably uniform allowing for the complex patterning of the feathers.

The species as a whole differs from *erckelii* and *ochropectus* in having a red bill and legs, the upper spur equal to or shorter than the lower. It has less black on the face and forehead, some U-patterning on the feathers of the mantle and breast and the abdomen largely white. In all the birds of the Arussi plateau south to Alghe (*F. c. castaneicollis*) this U-patterning is extensive on the back, wing-coverts and breast and clearly defined in black and white, mixed with some ochre and chestnut: Somali birds are similar but rather greyer (*ogoensis*). Birds from all the isolated populations west of Lake Zwai vary slightly (but may be grouped for convenience as *F. c. kaffanus*) but the U-patterning in all is less well defined and less extensive and the ochre is largely replaced by rich chestnut. An isolated population at Mega (*atrifrons*), less than 50 miles from Alghe where *F. c. castaneicollis* occurs, is quite unlike, being without any strong colour or pattern, the U-patterning being only faintly defined in brown and buff, and the throat and abdomen cream instead of white. This, like *ochropectus*, is a population whose taxonomic rank is questionable but Benson (1945: 393) found it was similar in habits, environment and voice to other forms of *F. castaneicollis* and it is therefore perhaps best regarded as a subspecies in spite of its very distinctive appearance.

There are unaccountably no representatives of the group in the juniper forests at Yavello (Benson, *op. cit.*), or apparently on the mountains of the southern Sudan, Uganda and northern Kenya (though they may possibly have been overlooked on the lesser known mountains, and unidentified francolins have been recorded from Mt. Kulal and Mt. Nyeri at the southern end of Lake Rudolf) but in the Aberdare Highlands and on Mount Kenya *F. jacksoni* is common near the edge of the forest and in the bamboo above 7,500 ft. It has also been found twice west of the Rift on the Mau Escarpment and in the Cherangani Mountains. It is very similar to the more chestnut and less heavily patterned populations of *F. castaneicollis* found in the west, but has the wings, back and tail a brighter more rufous brown, and the feathers of the upper mantle, breast and abdomen chestnut edged with white, with no black and white U-patterning. *F. jacksoni* has a scarlet eyelid: males usually have two spurs with the upper poorly developed. Birds of Mount Kenya (*F. j. pollenorum* Meinertzhagen, 1937) are rather darker than western birds (*F. j. jacksoni*), and in both populations there is individual variation in the extent of white below.

F. nobilis of Ruwenzori and the mountains from Kivu north to Lake Albert is rather smaller than the foregoing species and less patterned than any except the Mega population, *F. c. atrifrons*. It has the head, primaries and tail grey-brown and the mantle and wing-coverts deep maroon, with faint grey scalloping on the upper mantle: the throat is off-white and the rest of the underparts chestnut with some narrow grey or whitish edges or scallops replacing the broad white edges of

jacksoni: there is a conspicuous circle of red skin round the eye: like *F. jacksoni* and *F. castaneicollis* it has a red bill and legs but with the short upper spur of *jacksoni*. The width of the greyish edges to the chestnut feathers below varies individually but, from the limited series available, it seems that in the population of Ruwenzori (*F. n. chapini* Grant & Praed, 1934) they are consistently narrow.

The male of the Cameroon Mountain francolin, *F. camerunensis*, is very like *F. nobilis*, except that the maroon of the mantle and wing-coverts and the grey brown of the back are replaced by a rich dark brown, and the underparts are plain grey with some darker feather centres: the area of bare skin round the eye is more extensive. The female is quite different, being mottled and vermiculated above and below in black, dark brown and buff, with some dark brown or black and off-white U-patterning, on the mantle, breast and abdomen.

The last species of the group is *F. swierstrai* which is found associated with patches of evergreen forest in the Bailundu highlands and along the escarpment in Angola. It is isolated from all other members of the group by over 1,000 miles and, morphologically, is the species least readily linked with any other in the group. Both sexes have conspicuous white eyestripes (not found in other members of the group) and a dull brown mantle and wing coverts, concolorous with the back, but which in the female have irregular blotches and transverse markings of darker and paler brown: the male below is mainly white with the upper breast black contrasting with the white throat, and with the lower breast and abdomen streaked with black on the feather edges: some feathers of the flanks are black with a white U-pattern. The female below is mainly white with irregular black or brown blotches or bars, which are most heavily concentrated on the upper breast to form a mottled band and are sparse in the centre of the abdomen (see T aylor, 1960a: 142). The bill and legs are red or orange red as in most other species of the group but the male has commonly only one spur. It has no red skin round the eye.

EVOLUTION

The distributional pattern presented by these isolated populations associated with high altitude evergreen forest is only readily interpreted if these populations are regarded as relicts from a cold, wet era when the montane forest and the group as a whole had a more or less continuous distribution between the extreme points of which it is now found (Map 3A). Any retreat of the forest would cut off the outlying Cameroon and Angola populations from the eastern birds and they may therefore be presumed to have been isolated for the longest period, allowing greater opportunity for divergence.

Similarly the marked, but less extreme, divergence shown by *F. nobilis*, *F. jacksoni* and *F. castaneicollis kaffanus* is to be expected since the mountains of the Congo border, Kenya and southern Abyssinia are separated from each other by over 300 miles of comparatively low country. In Abyssinia, on the other hand, the problem is more complex for the divergence between the northern *F. erckelii* and the southern *F. castaneicollis* is extreme, yet they are not separated from each other by any greater distance or any greater natural barrier than there is between

the several isolated populations of *F. castaneicollis*. It seems possible that the interpretation of this pattern may be found in the ecological differences between the two species for, from the limited field notes available, it is apparent that *F. erckelii* alone of the Montane Group is not dependent on evergreen forest, being found widely in grassland. (I can find no information on whether it is also found in the evergreen patches within the range, and it is possible that it exploits both habitats.) Furthermore, the unusual degree of uniformity of colour and pattern in *F. erckelii* argues a continuity of range over a long period, so it can be expected that adaptation to this type of habitat, which has a less fragmentary distribution than evergreen forest, took place early in the history of the species soon after it was first isolated by a retreat of the forest. This adaptation would have raised an ecological barrier between proto-*erckelii* and proto-*castaneicollis* which would inhibit interbreeding in any subsequent era in which there was a sufficient spread of evergreen forest to reunite the scattered montane communities in Abyssinia.

It seems unlikely that such a spread has taken place within comparatively recent times, for there has been time enough for divergence between most of the isolated populations of *F. castaneicollis*. This divergence is particularly marked between the populations west and east of the Rift, *F. c. kaffanus* and *F. c. castaneicollis*, and in the isolated Mega population *F. c. atrifrons*, and it is likely that breaks were made earlier between these three groups than between the individual populations of the south-west.

But while *atrifrons* can be regarded without much hesitation as a population which has diverged from *F. castaneicollis*, any guess at the origin of *F. ochropectus* in (French) Somaliland is more doubtful, for it is closest morphologically to *F. erckelii* but has some characters of *F. castaneicollis* and is also a bird of evergreen forest. It could be postulated that, in isolation, it has descended without much variation from the common ancestor of *erckelii* and *castaneicollis*, or that it is a product of hybridisation between them at a later reunion. Although the distances that separate *ochropectus* from the neighbouring species are not great, the country between is so low and dry and it would require extreme climatic change to bridge it with forest or montane grassland, so that the first of these two alternatives seems the more likely.

There is no such formidable barrier between *F. c. erckelii* and the greyer *F. e. pentoni*, isolated in the Red Sea Hills, and the relatively slight divergence between them does not suggest lengthy isolation.

A summary of the evolution postulated is as follows:—

Stage 1. The group widespread in an era in which montane forest covered a large part of Africa (Map 3A).

Stage 2. With a retreat of montane forest proto-*swierstrai* and proto-*camerunensis* become isolated first and subsequently the ancestral stocks of the other species.

Stage 3. In isolation proto-*erckelii* becomes adapted to grasslands.

Stage 4. A limited spread of forest allows interbreeding within the ranges of proto-*nobilis*, proto-*jacksoni* and proto-*castaneicollis*, but though the ranges of proto-*erckelii* and proto-*castaneicollis* may join there is no interbreeding. Proto-*ochropectus* remains isolated.

Stage 5. The forest gradually retreats causing first a split between the populations of proto-*castaneicollis* east and west of the Rift, and isolating the Mega population, proto-*atrifrons*, and next the populations of south-west Abyssinia. Subsequently the forest retreats to its present limits and the country south of the Red Sea Hills becomes unsuitable for *erckelii*, isolating the population at Erkowit.

THE SCALY GROUP (MAP 4)

(*F. ahantensis*, *F. squamatus*, *F. griseostriatus*)

RANGE AND CHARACTERS

The range of the Scaly Group lies entirely within 15° of the Equator, and largely within the limits of the lowland forest in both Upper and Lower Guinea. Inside the forest these francolins are found in clearings and cultivations. Outside the perimeter of the forest there are scattered populations north to the Gambia in the west and to the Jebel Marra in the Sudan, east to Amani in north-eastern Tanganyika, south to the Vipya plateau, northern Nyasaland, and to the Benguela district in Angola. These scattered populations may be found in vestigial patches of lowland forest, riverine forest, montane forest or in cultivations in which there is sufficient cover in which to hide.

The members of the group are the plainest of the francolins, having little defined pattern or strong colour. The upper parts are mostly brown sometimes with underlying vermiculations and with indistinct patterning on the hind neck and mantle, the feathers having paler edges and darker centres varying from blackish to orange-brown. There is no defined pattern on the face and the throat is whitish. The remainder of the underparts are chiefly brown or creamy-buff with the colour and patterning varying in the different forms but all have very narrow darker edges to the breast feathers which give a scaly appearance. The bill is orange or red with some black or brown on the culmen or at the base, and the legs are orange-red, the males having one main spur and commonly a small upper spur in at least two of the three species. There is no marked sexual dimorphism but females tend to be more vermiculated than the males and in some forms tend also to be paler.

SPECIES AND POTENTIAL SPECIES

All forms are allopatric with the three recognised species clearly differentiated, but otherwise geographical variation in most of the range is not well defined and tends to be obscured by individual variation. The West African species (*F. ahantensis*) is found within the limits of the main block of the Upper Guinea forest from Sierra Leone to Ghana and in the part of the Lower Guinea forest lying west of the Niger. Scattered populations are found also in Portuguese Guinea and the Gambia (and might be expected in former French Guinea).

In *ahantensis* the upper parts are indistinctly vermiculated with some white U-patterning on the mantle, the feathers having blackish centres, occasionally with a reddish-brown shaft streak: the underparts are brown with white and darker brown U-patterning: the bill is orange with a black base.

The populations of Portuguese Guinea and the Gambia (*hopkinsoni* Bannerman,

1934) are slightly paler. On the map they appear to be separated from the main body by about 350 miles, but it is likely that scattered populations exist in suitable patches of thick bush along the rivers of (French) Guinea, and that variation will be found to be clinal.

The Niger appears to form a complete barrier between *ahantensis* on the west and *F. squamatus* on the east. The birds found within the boundaries of the forest from the Niger east to the Ituri (*F. s. squamatus*) are the least distinctly patterned of all the group having the upper parts indistinctly vermiculated with faint greyish U-patterning on the upper mantle, the feathers having blackish centres tinged with red-brown: the underparts are plain brown with a scaly pattern and ill-defined darker shaft streaks: the bill is red or orange-red with a darker culmen.

All the scattered populations outside the perimeter of the Guinea forest, namely those from the Sudan, Abyssinia, eastern Kenya, Uganda, western Tanganyika, the southern Congo and north-eastern Angola, are sufficiently alike to be united under the subspecific name *schuetti*. They differ from *F. s. squamatus* in being less vermiculated, with the pattern on the mantle slightly more clearly defined and with more red-brown in the centre of the feathers: below they have a less scaly appearance, the feathers of the abdomen having whitish edges giving an irregular streaky effect. Within this large range there is much individual and some local variation in the amount of white below and in the tone of the browns but no significant geographical variation, although populations are found in varying habitats, in vestigial patches of lowland and gallery forest and in the lower levels of the montane forests of the east Congo (up to about 6,500 ft.), and in the mountains of the southern Sudan (up to 8,500 ft.). In Uganda and Kenya, where much of the forest has been cleared within the last sixty years, *F. squamatus* has become largely adapted to cultivations, but is also found in montane forest up to 9,500 ft. (Mt. Elgon).

West of the Rift in Kenya, southwards to Kilimanjaro, Monduli and Mount Meru in north-eastern Tanganyika, the birds become increasingly darker and greyer, with often less white on the abdomen, especially in the males. The darkest, plainest populations are found on Kilimanjaro (up to 6,500 ft.) (*maranensis*) and in the Chyulu Hills.

Although the range of Scaly Francolins in East Africa is now discontinuous and in these eastern districts the populations are isolated on the mountains (and may be diverging) the variation exhibited appears fundamentally clinal from a time when distribution was continuous. However, only 150 miles south-east of Kilimanjaro birds from the Usambara Mountains (*usambarae*) show a consistent difference, having the lores, eye-stripes and cheeks freckled with black and white instead of being an ill-defined brown. This marking has been described as even more pronounced in a single, rather paler, specimen (the type of *uzungwensis*) from Kigomo, Uzungwe Mountains, in south-western Tanganyika, 350 miles to the south. There are no records of Scaly Francolins from the country between Amani and Kigomo, much of which is totally unsuitable, but it might be expected in forest patches of the Nguru and Uluguru Mountains.

Another isolated population is found still further south on the Vipya plateau of central Nyasaland, in forest between 3,000 and 6,000 ft. (*doni* Benson, 1939), which

is a richer red-brown in the centres of the feathers both above and below, and has very few white streaks on the abdomen; there is some black in the lores and eye-stripe. The colour, but not the extent of the red-brown patterning in the mantle, is matched in a few individuals of *schuetti* from various parts of its range, but none approaches this colour below.

The third species of the Scaly Group, *F. griseostriatus*, is confined to the strip of rich vegetation with vestigial patches of forest which is associated with the escarpment in western Angola. It is the most distinct member of the group having the feathers of the mantle and wing-coverts chestnut broadly edged with grey, and the rest of the upper parts faintly vermiculated, as in *F. s. squamatus* and *F. ahantensis*, but paler: below the feathers of the breast and flanks are chestnut edged greyish or creamy buff and the abdomen is plain creamy buff. While the coloration is brighter and more contrasting, the pattern of the feathers of *griseostriatus* is fundamentally the same as in the other two species. The bill is mainly blackish on the upper mandible with a bright red base, and below is orange-red: the legs are orange-red, and the three males examined have only a single spur.

EVOLUTION

The chief features of the distributional pattern of the Scaly Group are the two specific divisions which separate *ahantensis* and *griseostriatus* from *squamatus*; the vast areas in which *squamatus* exhibits no significant variation: and finally the indications of speciation in the eastern populations. The fact that the ranges of *F. ahantensis*, and *F. s. squamatus* coincide so closely with the limits of the main blocks of lowland forest suggest strongly that glades and clearings in this type of forest must be regarded as the natural habitat for the group, and that the populations found outside the perimeter of the forest are relicts from a period in which the forest extended to the extreme limits of the range of the Group. The occurrence of these populations in montane forest, up to at least 9,500 ft. on some mountains, and the rapid adaptation of the birds in Kenya to cultivations indicate, however, that their requirements are not rigid as long as sufficient cover is available. A wide spread of montane forest might, therefore, not be wholly disastrous for the Scaly Group, though they could not expect to compete entirely successfully with members of the Montane Group in these conditions. (It is perhaps significant that the highest altitudes at which Scaly Francolins have been found are on Mount Elgon, which has apparently no representative of the Montane Group.)

It seems likely, therefore, that prolonged dry eras have been the chief factors in speciation. In some such periods (possibly coincidental) early in the history of the group proto-*ahantensis* could have been isolated from proto-*squamatus* by a belt of savanna stretching to the coast between the Niger and the Volta, and proto-*griseostriatus* isolated along the escarpment of Angola, where moister conditions prevailed, while the interior of the country was dry (Hall, 1960b). With a return of wetter conditions in West Africa proto-*ahantensis* spread eastwards. The lack of divergence between populations on either side of the present gap in the forest east of the Volta lends support to the conclusions cited by Moreau that the gap between

the two blocks of forest was formerly further east in the neighbourhood of the Niger delta. The Niger itself at present lies between the two species, and since there can be little temptation for sedentary birds such as francolins to fly across a broad river it can be regarded as a barrier sufficiently formidable to inhibit interbreeding. It is possible that the Lower Congo could have acted as a similar barrier between *proto-squamatus* and *proto-griseostriatus* if in a wet era the escarpment forests of Angola were reunited with the forest of Gabon and Cabinda.

In *F. squamatus* the remarkable lack of variation in the whole species argues that the last spread of forest which linked the present outlying populations was of comparatively recent date. If degree of divergence can be accepted as a guide to time then it can be postulated that the earliest populations to be isolated by the retreat of the lowland forest would be those of Nyasaland and Tanganyika: but in this instance especially this precept must be posed very tentatively for the isolated populations concerned have also become adapted to rather different conditions at higher altitudes which might accelerate divergence. Since the most geographically remote of the remaining populations, those of the Jebel Marra (known from one specimen only) and southern Abyssinia, do not differ significantly from typical *schuetti* in north-eastern Angola and the southern Congo, the forest may have persisted longest in north-eastern Africa.

Finally the distinction and the fairly sharp transition between *squamatus* and *schuetti* on the perimeter of the Congo forest merits attention. It suggests that at some time western and eastern birds were divided (presumably in a dry era) and on reuniting the eastern birds tended to favour rather more open habitat on the forest fringes, and the western birds clearings in the deep forest.

A summary of the evolution postulated is as follows:—

Stage 1. The group developing in lowland forest, and probably extending to East Africa.

Stage 2. In a dry era *proto-ahantensis* in the Upper Guinea forest becomes cut off from *proto-squamatus* in the Lower Guinea forest somewhere in the region of the Niger. *Proto-griseostriatus* in the escarpment forests of Angola also becomes cut off from *proto-squamatus*.

Stage 3. In a wetter, more favourable, era, the group spreads again but no interbreeding takes place between the incipient species, the barriers formed by the Niger and Lower Congo possibly reinforcing any tendency to genetic isolation that has developed while they have been separated.

Stage 4. A dry era divides the Lower Guinea forest into a western block, in which *proto-squamatus* subsp. develops and an eastern block in which the birds become adapted to slightly less humid conditions. These eastern birds, *proto-schuetti*, keeping more to the forest fringes when the two are reunited.

Stage 5. A wide spread of lowland forest extends the range of *proto-ahantensis* to the Gambia, and *proto-squamatus* sp. to embrace all the outlying localities at which it is found at present (Map 4A).

Stage 6. With the retreat of the forest, populations become isolated first in Nyasaland, *proto-doni*, and Tanganyika, *proto-uzungwensis* and *proto-usambarae*, then on the mountains of the Kenya/Tanganyika border, and finally in the Sudan, Uganda

and Abyssinia. These isolated populations survive in isolated patches of lowland and riverine forest, and also become adapted to montane forest up to high altitudes, especially where there is no competition from members of the Montane Group, and, in some areas, to cultivations.

In West Africa populations of *ahantensis* become isolated in the Gambia and Portuguese Guinea and the main block of the species is divided by a break in the forest in the region of the Volta.

THE VERMICULATED GROUP (MAP 5)

(*F. bicalcaratus*, *F. icterorhynchus*, *F. clappertoni*, *F. hildebrandti*, *F. natalensis*, *F. hartlaubi*, *F. harwoodi*, *F. adspersus*, *F. capensis*)

RANGE AND CHARACTERS

The Vermiculated Group is the most widespread of all the African groups. I regard it as consisting of a superspecies (containing six allopatric species) and three related species. The superspecies has a more or less continuous distribution from Senegal to Eritrea and southwards to Natal with outlying populations in Morocco and in the mountains of South West Africa and southern Angola. Of the three extraneous species one (*F. harwoodi*) is confined to a small area of Abyssinia almost encircled by the superspecies: the second (*F. adspersus*) replaces the superspecies in northern Bechuanaland but is partly sympatric with the outlying population in South West Africa: the third (*F. capensis*) is completely isolated in the extreme south.

The ecology of the group is variable and will be discussed in detail under the individual species but it can be said in general that from West Africa to Abyssinia and Uganda the members of the superspecies (*F. bicalcaratus*, *icterorhynchus* and *clappertoni*) are birds of grasslands and cultivations in the woodland, acacia savanna and steppe belts. However, in east and southern Africa this habitat is largely occupied by members of other groups, in particular *F. afer* of the Bare-throated Group (Chapin 1932: 714), and it appears that members of the Vermiculated Group have been driven into more rocky country on hillsides and into thickets in river valleys and the distribution is consequently more broken (compare Maps 2 and 5).

In choosing the term "vermiculated" as the descriptive name for this group I have given emphasis to the most striking character which the majority of the component forms have in common although in some subspecies of *F. clappertoni* the vermiculations are largely or wholly replaced by extensive U-patterning. All members have brown or grey-brown heads, backs, wings and tail, with lighter vermiculations and/or V- and U-patterning, and sometimes some rufous mottling: the lores are black or blackish and most forms have a white eye-stripe: the underparts are patterned with dark brown (and sometimes chestnut or maroon) on a whitish or cream background, except in the females of the two sexually dimorphic forms which are plain orange-ochre below: the colours of the bill and legs, and the colour and extent of bare facial skin, is variable and so is the number of spurs (see Table 1).

SPECIES AND POTENTIAL SPECIES

The superspecies consists of six clearly differentiated forms which are usually regarded as species, though it can be argued that two of these, *F. hildebrandti* and *F. natalensis*, could be treated as conspecific. The three northern members, *F. bicalcaratus*, *F. icterorhynchus* and *F. clappertoni*, form a homogeneous assemblage occupying grasslands and savannas of various types. *F. bicalcaratus* is the representative in West Africa, being common in the acacia and woodland belts from Senegal to the Cameroons, extending also into cleared parts of the Upper Guinea forest. There is also an isolated population in Morocco. Above, it is faintly vermiculated with extensive V- or U-patterning on the mantle and wing-coverts: below, each feather is cream with some chestnut on the edges and with a black drop-shaped centre that is broken by small cream "windows" (Fig. 1, 15), giving a partly streaked and partly spotted effect: the bill and legs are greenish, and two fairly well-developed spurs are common in the males.

The Morocco population (*ayasha*) is not conspicuously different, though isolated by 1,500 miles, but may be slightly more rufous and with rather smaller "windows" in the patterning below. Other variation in the species is clinal and will be discussed later.

In the Cameroons, at about longitude 15°E., *F. bicalcaratus* is replaced abruptly (but not apparently along any ecological boundary) by a plainer bird, *F. icterorhynchus*, which is more vermiculated and less V-patterned above, and which is irregularly V-patterned, blotched or spotted with dark brown below: the bill and legs differ from *bicalcaratus* in being mainly orange, and there is a small patch of yellow skin round the eye. Its range extends eastwards through the woodland belt (Map 11, types 16 and 17) to Uganda, where a few specimens are found which have some chestnut streaks on the flanks (as in the type of "*F. ugandensis*"). In the acacia belt to the north (Map 11, type 20) *F. clappertoni* replaces *F. bicalcaratus* between northern Nigeria and Lake Chad, and replaces *F. icterorhynchus* in the Sudan. It is common also in the Nile and Blue Nile valleys and on grassy hillsides of western Abyssinia and Eritrea below 7,000 ft. (above which it is replaced by the montane francolin, *F. erckelii*). Western birds (*F. c. clappertoni*) are very similar to *F. icterorhynchus* above but a more orange brown, while below they resemble *F. bicalcaratus* except that there are no "windows" in the dark feather centres and the feathers are edged with maroon rather than chestnut. In the Nile valley and southern Sudan birds become darker and greyer, less vermiculated, but heavily U-patterned above and more heavily patterned below on a whiter ground. In the Blue Nile valley and eastwards birds lack vermiculations entirely but are clearly and regularly V-patterned above and on the breast, giving a lanceolate appearance, and they lack the moustachial streak which is present in the western birds.

A single specimen collected at "Ngeem", Lake Chad (possibly Nguigmi on the north-west edge of Lake Chad), the type of "*F. tschadensis*", is very like some of the specimens of *F. clappertoni* from the Nile valley but the underparts are more buffy and lack any maroon markings, and it is rather less heavily patterned on the back. Neumann suggested (*cf* Bannerman, 1: 327) that it is a hybrid between *F. clappertoni* and *F. icterorhynchus*. Since *F. icterorhynchus* does not now apparently occur as

far north as this, and since this specimen is rather more heavily patterned than the northern populations of *icterorhynchus* and *clappertoni* it might perhaps be better regarded as an aberrant specimen that indicates the close relationship of the two species.

East and south of Lake Victoria *F. icterorhynchus* is replaced by *F. hildebrandti*, which is a bird largely associated with rocky ground and thickets in river valleys and on hillsides, from sea level to about 8,000 ft., and which is found equally in the acacia savanna and the brachystegia woodland belts. It is common from central Kenya south to the Tabora and Dodoma districts of Tanganyika but in the southern part of Tanganyika and northern Mozambique its distribution is sporadic: however, it is again common in Nyasaland at varying altitudes, and in the upper Luangwa valley. The males are very like *F. icterorhynchus* above, but have more solid, blotchy, brown markings below: the bill is reddish with a brown culmen and yellowish base, and the legs reddish. The female is quite different having the underparts plain orange ochre. The sexual differences are most complete in the most southerly birds from southern Nyasaland, Mozambique and south-west Tanganyika (*F. h. johnstoni*) in which the female has no patterned plumage on either the upper mantle or the breast, whereas those from most of Kenya (*F. h. altumi*) have some patterned "male" plumage on both. Females from the centre of the range (*F. h. hildebrandti*) are intermediate, having the patterned feathers mostly confined to the upper mantle.

F. hildebrandti reaches the southern limits of its range in the Luangwa and Shire valleys, and is replaced further south by *F. natalensis*, a bird with apparently the same ecological preferences. Birds from the Transvaal and Natal and the southern parts of Southern Rhodesia (*F. n. natalensis*) differ from *hildebrandti* in having the sexes alike, the backs darker brown and more heavily patterned and vermiculated and having regular double U-patterning below, unlike the brown blotches of the male *hildebrandti*. The bill and legs of *natalensis* are similar to those of *hildebrandti* except that there is no black on the culmen and the male has commonly one spur and the female none, whereas in *hildebrandti* the male has commonly two (once three) spurs and the female one or two vestigial spurs. However, the intensity and regularity of the patterning, particularly in the females, decreases northwards, showing some approach to *hildebrandti*. The populations of the northern districts of Southern Rhodesia, the Zambezi valley and the Luangwa valley (*neavei*) are plainer and more rufous above and the females tend to have the underparts washed with buff, the abdomen plainer and the U-patterning less defined giving a more spotted or streaked effect, but there is much individual variation.

As far as is known the ranges of *F. hildebrandti* and *F. natalensis* only approach each other in two areas, in the Luangwa valley between latitudes 12° and 13°S and in the neighbourhood of the Shire/Zambezi confluence. In the Luangwa valley there is some indication that the two may sometimes interbreed, or have interbred in the recent past, for some of the specimens of *natalensis* are more blotched, less U-patterned below than those of *F. n. neavei*, and some of the females are washed with buff below and have plainer abdomens (see Benson and White, 1957: 138): one male from Jumbe (13° 16'S., 32° 07'E.) lent by the National Museum of

Southern Rhodesia is close to *F. n. neavei* below but has, like *hildebrandti*, a dusky ridge to the culmen and two spurs. Nevertheless, there are in this area specimens typical of the two forms taken from within 50 miles of each other so it is probable that there is only sporadic interbreeding.

In the Zambezi/Shiré area the situation seems rather different. *F. natalensis* has been collected from points along the Zambezi as far down as Tambara (60 miles below Tete) but not as low as the junction with the Shiré, and not from the left bank below the junction of the Mushonganende River, 280 miles above Tete. Within 40–60 miles of Tambara *F. hildebrandti* has been collected in southern Nyasaland and neighbouring Mozambique at Zobue, "on rocky hillsides" (Vincent 1934: 336), on Mlunganyama hill "at 500 ft. but not at 200 ft." (Benson, C. W. & F. M., 1948: 3), on Mwananbidzi Hill at 2,500 ft., and near Port Herald in the Shiré valley (Long, 1960: 100), but not as far down the Shiré as the confluence. There is no evidence in this area of interbreeding between *F. natalensis neavei* and *F. hildebrandti* and it has been suggested that here the Zambezi itself, which is as much as two miles wide when in flood, may be a barrier (Benson, *et alia*: in press).

The last member of the superspecies, *F. hartlaubi*, is confined to the mountains of northern South West Africa and southern Angola and is strictly a bird of the rocks. It is the smallest member of the group and has distinctive rufous mottling above. The females are rufous below like those of *F. hildebrandti* but the male is finely streaked from chin to abdomen in brown and white. The bill is brownish above and yellow below and at the base: the legs are yellow with spurs poorly developed but often with two present vestigially in both sexes.

The first of the three members of the group which are not included in the superspecies is a francolin about which little is known, *F. harwoodi*. Only males have been collected and from only three localities, all in the gorges of the Upper Blue Nile or its tributaries. Of members of the superspecies it resembles *F. natalensis* most closely, being similar above but with more defined U-patterning on the nape, and below having similar double U-patterning, but rather darker and more clearly defined and extending to the chin, and being absent from the centre of the abdomen, which is cream. It is distinctive in lacking the white eye-stripe but having a circle of bare scarlet skin round the eye. The bill is recorded as red but from the appearance of skins probably has a black culmen; the legs are red with two fairly well-developed spurs. *F. harwoodi* appears to be cut off from other members of the group by the presence of the montane francolin *F. erckelii* on the plateau above the gorges, in the type of open country which, at lower altitudes, is occupied by *F. clappertoni* both to the north and the south.

In southern Africa along the borders of Rhodesia and Bechuanaland the superspecies (represented by *F. natalensis*) is replaced in similar habitat by *F. adspersus*, which ranges westwards through both acacia savanna and steppe (Map 11, types 20 and 25) to South West Africa where it overlaps the range of the isolated member of the superspecies, *F. hartlaubi*. Here the two forms are found in the same localities but differ in their ecology and habits, *adspersus* living in coveys along watercourses and *hartlaubi* usually in pairs on the rocks. *F. adspersus* is a rather different-looking bird from those members of the group that have been discussed: its appearance is

grey, the pattern being composed of minute vermiculations on the upper parts and with broader black-and-white vermiculations over all the underparts. It has no eyestripe but an area of bare yellow skin round the eye: the bill and legs are orange-red, the male having usually a single long spur.

The last member of the Vermiculated Group, *F. capensis*, is isolated in the extreme south-west. Like many other members of the group it is found in thick cover in rocky river valleys chiefly in the coastal districts of the Cape. It is not known from Little Namaqualand (possibly because of the lack of suitable rivers) but has been recorded from the gorge of the lower Orange River at Assenkjer. It is the largest member of the group and most like *F. natalensis* and *F. harwoodi* in the predominance of brown and white double U- or double V-patterning. However, in *capensis* the patterning is distinctive in being composed of very fine irregular white lines on most of the back (the rest being vermiculated), and similar on the underparts but with distinct white shaft streaks, giving a streaky effect: it has no eye-stripe and no bare skin round the eye: the bill, as in *hildebrandti*, is red with a dark culmen, and the legs red, the male having one or two spurs and the female one.

OTHER VARIATION

In *F. bicalcaratus* variation is largely clinal, the palest birds being found in the drier savanna areas and the darkest and most heavily patterned in the cleared parts of the forest areas in southern Cameroons. Among the dry country birds those from Senegal, Gambia and the hinterland of Ghana (*bicalcaratus*) are paler with more rufous heads than those of northern Nigeria and northern Cameroons (*adamauae*). The birds from within the borders of the Upper Guinea forest from Sierra Leone to Ashanti (*thornei*) are slightly whiter, less creamy below than those within the borders of the Lower Guinea forest from south-eastern Nigeria and southern Cameroons (*ogilviegranti*) which become increasingly dark eastwards. Birds from Accra, between the two forest blocks, are closer to *bicalcaratus* than to *thornei*: those of most of southern Nigeria are intermediate between *adamauae* and *ogilviegranti*. The isolated *ayesha* in Morocco (already discussed) is closest to the paler birds above but has heavier patterning below.

In *F. icterorhynchus* variation is clinal and ecological, pale, lightly patterned birds being found in the southern Sudan and in the region of the Albert Nile in northern Uganda (*icterorhynchus*): dark, heavily patterned birds are found in the more humid areas from the Oubangi and Uelle to southern Uganda (*dybowskii*).

In *F. clappertoni* the clinal variation is greater than in the two previous species, and features some changes in pattern that warranted discussion in the main section. West of the Nile and in the Nile Valley the paler, less patterned *clappertoni* merges through the intermediate *heuglini* to the dark U-patterned *gedgii* of the southern Sudan. Among the more V-patterned, lanceolated populations of the east, those of Eritrea, and northern Abyssinia (*sharpii*) are pale above (though not as sandy as *clappertoni*), those of south-western Abyssinia (*nigrosquamatus*) are darker and more patterned, and those of the Blue Nile valley (*konigseggii*) are somewhat intermediate, closest to *sharpii* but with a greater suffusion of black markings below.

In the southern populations of *F. natalensis* there is some variation according to the habitat, darker, more patterned birds being found in the richer vegetation of Natal, Zululand, and the Zoutspansberg, and paler birds in the drier savanna country of the Transvaal (see Clancey, 1953: 59). (Since the range of the darker birds is discontinuous it is impracticable to distinguish the two variations by name.)

The available series of *F. hartlaubi* is inadequate for detailed study, but it would seem that the populations of southern Angola (*hartlaubi*) are rather smaller than those of South West

Africa, and that the western birds from the Kaokoveld and Erongo (*crypticus* Stresemann, 1939) are rather paler than those from the Waterburg and Otavi further east (*bradfieldi*).

EVOLUTION

It has already been suggested that the rather different ecology of the northern members of the Vermiculated Group compared with those from Kenya southwards may be due to competition with the Bare-throated Group, and this possibility has considerable bearing on the interpretation of the pattern presented by the ranges of the various species. I believe, for example, that while the present can be regarded as generally favourable for the Vermiculated Group as a whole, it is even more favourable for the Bare-throated Group and that the distribution of the southern vermiculated species is heavily restricted because of this, especially in the areas where alternative habitats to the savanna grasslands are limited.

This would account for the absence of any member of the group from the grasslands south of the Congo forest, also for the sporadic distribution in eastern Africa, and possibly also for the limited ranges of *F. natalensis* and *F. capensis* in the coastal districts of the south-east, where the gap between them is occupied by the bare-throated *F. afer*.

In the north-east it is apparent from the isolated population in Morocco that the group is not at present as widespread as it has been at some time in the not distant past (to judge by the lack of divergence in the Morocco population). Elsewhere in the north the range appears to be expanding, for there is good reason to suppose that *F. clappertoni* has only recently extended its range in the acacia savanna south of the Sahara, where it has supplanted *F. coqui* (see discussion under Red-tailed Group and Maps 5 & 8), and also has recently extended its range eastwards towards the Red Sea coast, cutting off the Erkowit population of the montane francolin (*F. e. pentoni*) from the main body of the species (compare maps 3 and 5).

From the foregoing it can be assumed that grasslands and scrub in savanna and woodland are the natural habitat for the group, but it is adaptable: the presence of several members in areas where the rainfall is under 10 inches a year shows especially that it can be tolerant of dry conditions if there is adequate cover in watercourses. It is likely, therefore, that humid eras in which there has been a wide spread of forest have been less favourable to the group than the dry eras, and that it is chiefly in these wet eras that the group has been split and speciation has developed in the isolated populations. The morphological differences between *F. adspersus* and other members of the group, combined with the fact that it has diverged sufficiently to be able to live alongside another member, *F. hartlaubi*, in complete ecological segregation, suggest that probably the group developed in the east and south-east and that proto-*adspersus* was isolated earliest from the original stock. This could conceivably have taken place at the time when a spread of montane forest linked the Natal forests with those of Southern Rhodesia and Nyasaland, cutting off proto-*adspersus* in the Kalahari/South West African region. Proto-*capensis* and proto-*harwoodi* can be presumed also to have been isolated at an earlier period than any of the six members of the superspecies, but several factors could have caused their segregation. Proto-*capensis*, as suggested, could have been cut off by the

intrusion of the bare-throated *F. afer*. *F. harwoodi* on the other hand appears to be a "relict" population that has survived in the Blue Nile Gorges at a period when the group was overrun on the plateau above. The fact that the high parts of the plateau immediately surrounding the range of *harwoodi* are at present occupied by *F. erckelii* of the montane group suggests that it was first split from other members of the group in an era when montane conditions prevailed all over the plateau, as they do now.

Proto-*hartlaubi* in South West Africa may also have been cut off at an early date from the remainder of the superspecies, in which case it must be regarded as a coincidence that it has diverged along the same very distinctive lines (with marked sexual dimorphism) as the Tanganyika population, *hildebrandti*. It seems more likely that, following the periods in which *adspersus*, *capensis* and *harwoodi* were isolated, there was a period which favoured the superspecies, during which it became widespread through the grasslands of the tropics and south to Natal and the Transvaal. Meanwhile, proto-*adspersus* had become adapted to rather drier conditions in acacia steppe to the south-west. A subsequent drier era in southern Africa which spread acacia steppe through the Limpopo and Zambezi valleys could isolate proto-*natalensis* from the rest of the superspecies at a time when proto-*hartlaubi* and proto-*hildebrandti* were still linked. A further spread of steppe northwards bringing competition with proto-*adspersus* or a spread of the Bare-throated Group might then eliminate the superspecies from the areas between the Rhodesias and South West Africa, where there is little alternative habitat. The mountains of the west, however, would provide sufficient ecological variety for proto-*hartlaubi* to find a different habitat and co-exist in South West Africa with proto-*adspersus*, and in southern Angola with the bare-throated *afer*.

The tendency to approach *hildebrandti* shown by the Zambezi population of *natalensis* (*neavei*) suggests that these birds are either closest to the ancestral stock of *natalensis/hildebrandti* or else are the result of a period in which the two had become reunited after their distinctive characteristics had developed, but before there was any bar to free interbreeding. However, the lack at present of an intermediate population showing all stages of intergradation between *hildebrandti* and *natalensis* suggests that the ranges of the two were again separated in the not too distant past: the presence in the Luangwa valley of a few apparent hybrids among otherwise typical birds indicates that there has been only sporadic interbreeding now that the ranges again join. Minor fluctuations in climate would serve to bring about this splitting and reuniting.

The differences between the various populations of *hildebrandti* are not great enough to suggest any lengthy periods of isolation, but, combined with the present discontinuous distribution, indicate a limited amount of splitting and reuniting since the species developed. The greater amount of "male" plumage exhibited by the females of *hildebrandti* in western Kenya (*altumi*) indicates some approach to *F. icterorhynchus* of Uganda, suggesting that the break between them was at a comparatively recent date.

The three northern members of the superspecies, *icterorhynchus*, *clappertoni* and *bicalcaratus* form a homogeneous and completely allopatric assemblage from which

it can be postulated that the present extensive range has not been occupied for a long period, since otherwise climatic fluctuations would have caused complex splitting and rejoining of populations over such a wide area. To interpret the main lines of the pattern it is only necessary to visualise one period in which the ancestral stock of the three members spread westwards from Abyssinia to Senegal, followed by one unfavourable period in which it was divided into a western (proto-*bicalcaratus*), central (proto-*icterorhynchus*), and eastern (proto-*clappertoni*) population. This period seems likely to have been a humid one in which Lake Chad was extensive and forest extended from its southern tip southwards, forming a north-south barrier between the western and central parts of the savanna belt. At the same time it can be postulated that there would have been sufficient riverine forest along the Nile to form a second barrier further east, and that forest in Kenya and Uganda cut off proto-*icterorhynchus* from proto-*hildebrandti* in the south. Speciation developed in the three pockets and was almost complete when dry conditions returned. Proto-*clappertoni* became adapted to rather drier conditions than the other two species and spread eastwards over the Nile north of proto-*icterorhynchus*. The differences in pattern between the eastern and western populations of *clappertoni* suggest that at some subsequent period the Nile and its tributaries again formed a barrier between east and west, allowing birds with the distinctive V-patterning of *F. c. sharpii* to develop in the north-east. At present it appears that *clappertoni* is extending its range westwards, north of the ranges of *icterorhynchus* and *bicalcaratus*, at the expense of the red-tailed *coqui*.

In the west it is apparent that there must have been a period when sufficiently humid conditions prevailed along the coast to allow the francolins to spread to Morocco. The lack of marked divergence in the Morocco population (*ayesha*) suggests that this period was of a more recent date than the humid period postulated for the isolation of the ancestral stocks of the three northern species.

A summary of the evolution postulated is as follows:—

Stage 1. Ancestral stock of the group develops in the east and south-east.

Stage 2. Proto-*adspersus* isolated in the south, possibly by a spread of montane forest.

Stage 3. The rest of the group extends northwards to Abyssinia, and widely through grasslands south of the Congo. Proto-*capensis* isolated, perhaps by competition with the Bare-throated Group.

Stage 4. The group spreads westwards to Senegal but withdraws from the high plateau of Abyssinia, which is occupied by the Montane Group, leaving a relict population in the Blue Nile gorges, proto-*harwoodi*.

Stage 5. (South). Proto-*natalensis* isolated, possibly by extension of acacia steppe in Limpopo or Zambezi valleys bringing competition with proto-*adspersus*.

Stage 5. (North). Proto-*bicalcaratus* in the west, proto-*icterorhynchus* in the centre and proto-*clappertoni* in the east, isolated from each other, probably by a belt of forest extending northwards to Lake Chad (at a time when its area was more extensive), and by riverine forest in the Nile valley. Proto-*clappertoni* becoming adapted

to drier conditions than the other two species. Forest in Uganda and Kenya separates proto-*hildebrandti* from proto-*icterorhynchus*.

Stage 6. (South). Proto-*hartlaubi* isolated in the mountains of South West Africa and Angola, possibly by an invasion of the central areas by proto-*adspersus* or by the Bare-throated Group.

Stage 6. (North). Minor fluctuations, allowing proto-*clappertoni* first to spread westwards across the Nile and then splitting into a western and eastern population, possibly during a return of more humid conditions when the Nile valley again became a barrier.

Stage 7. (South). Minor fluctuations causing rejoining and re-splitting of proto-*natalensis* and proto-*hildebrandti*, and isolating populations of *hildebrandti* for short periods.

Stage 7. (North). A humid period in which proto-*bicalcaratus* spreads to Morocco, followed by a drier period in which the Morocco population is isolated.

Stage 8. (South). The ranges of *natalensis* and *hildebrandti* rejoin, at least in the Luangwa valley, and there is sporadic interbreeding.

Stage 8. (North). In the Sudan *clappertoni* spreads westwards through the drier acacia belt.

THE STRIATED GROUP (MAP 6)

(*F. sephaena*, *F. streptophorus*)

RANGE AND CHARACTERS

The Striated Group is unlike all others in consisting of only two species which are partly sympatric. The range of the group as a whole is mainly in eastern Africa, from Somalia to Natal, but extending across to South West Africa and southern Angola, and with an isolated population in the Cameroons.

Both species are mainly brown above with some chestnut, black and white pattern in the collar, and white shaft streaks on the mantle: the eye-stripes are white, edged with black and there is some chestnut on the sides of the face: the throat is white bordered with chestnut: the underparts are creamy buff with contrasting maroon, chestnut, or black-and-white patterning on the breast (different in the two species) and lighter patterning on the flanks and abdomen.

The habitat of the two species is different and will be discussed later.

SPECIES AND POTENTIAL SPECIES

The two species are quite distinct both ecologically and morphologically. *F. streptophorus* has a puzzling distribution, being found commonly in the grasslands and "orchard bush" of northern Uganda and sporadically in north-western Kenya usually on stony scrub-covered hillsides (Jackson, 1938: 241). In north-western Tanganyika Dillingham has found it also in clearings of brachystegia. These are the only areas from which it is known in the east but 1,500 miles to the west a single specimen was obtained by Bates among grass and rocks between 3,500 and 4,000 ft.,

in the Cameroon highlands 40 miles west of Fumban (on the borders of former British and French Cameroons).

It is a darker bird than *F. sephaena* the back being grey-brown with dark brown patches and with fewer and narrower white shaft-streaks. It has a solid chestnut collar on the hind neck above a broken black-and-white collar of barred feathers; there is a considerable amount of chestnut in the facial pattern but only a narrow band bordering the base of the throat: the feathers of the breast are barred black and white occasionally with a chestnut tip: the remainder of the underparts is pale cream marked with some dusky vermiculations and broad blackish streaks on the flanks: the bill is black with yellow at the base and the legs yellowish with only a vestigial spur in the males. The sexes are alike. The Cameroon bird is like those of East Africa but smaller (wing 1♂ 145 against 6♂ 151-160).

In northern Uganda, where both species are found, Pitman tells me that *sephaena* is strictly confined to the driest areas of scrubby thorn country while *streptophorus* is in savanna grasslands. Both Jackson (1938: 241) and Dillingham (*in litt.*) stress that the call of *streptophorus* is quite unlike that of any other francolin known to them, and is a melodious trill or whistle. Dillingham on the other hand found *sephaena*'s call closer to other francolins though Vincent, on a label of a bird from Swaziland, describes it as "a loud piping trill" and Benson tells me he has found it very variable, Rhodesian birds being hardly recognisable as the same species as those in Abyssinia. Comparison between the eggs would also be useful for Pitman confirms Jackson's statement that the eggs of *sephaena* are exceptionally hard, and it would be interesting to know if those of *streptophorus*, at present unknown, have the same character.

F. sephaena is widespread in the acacia savanna and steppe from eastern Abyssinia and (British) Somaliland westwards to the Albert Nile, southwards through Kenya and along the Tankanyika coast to Mozambique and Natal, westwards to South West Africa and southern Angola. It is never far from water and in the driest parts of the range is confined to watercourses.

Above it is a rich red-brown with broad white shaft-streaks: the chestnut collar is broken with white and the patterned feathers of the upper mantle are rich dark brown or blackish with elliptical white centres: the females are slightly vermiculated. There is no black on the underparts, the feathers of the breast being cream with triangular chestnut or maroon markings on the tips: the bill is wholly black and the legs carmine, the males having a single long sharp spur.

The birds here designated as *F. sephaena* have sometimes been considered to belong to two species, for two distinct types are found, one, mainly coastal, which has fine, drop-shaped maroon streaks on the abdomen, and the other in which the abdomen may have some dusky patterning but which has no maroon streaks. In the Shiré valley of southern Nyasaland birds of the two types appear to behave as species being found close to each other without an ecological division, but without any intergrading: specimens from the southern tip of Lake Nyasa and eastwards are streaked, and so are those from the lower Shiré valley at Chiromo and Tangadzi, but a specimen from Lengwe, 35 miles upstream, is unstreaked, as are those from all localities westwards in the Zambezi valley (Benson, C. W. and F. M., 1948: 3).

In northern Tanganyika a similar clear division is found between the two types, birds from inland, at altitudes above 1,500 ft., being unstreaked, those from the coastal plain being streaked. However, from the Kenya boundary northwards there is no clear division either geographically or morphologically: in western Kenya, southern Abyssinia (Benson, 1945: 391) and throughout Somalia both types are found, as well as some intermediates with sparse, fine streaks. In (British) Somaliland streaked birds predominate at lower altitudes near the coast but both types are found in the highlands and streaked specimens have been found as far inland as Harar in north-eastern Abyssinia. There is no evidence that the two types behave here as species and it is more probable that they represent a hybrid population. (For this population it is convenient to use the name *spilogaster*, which was given to a streaked bird from Harar—see Rand, 1950: 384 while *rovuma* should be confined to the unmixed streaked populations from Tanganyika southwards.)

It will be seen from the map that inland birds of the unstreaked type are found in two blocks from northern Tanganyika northwards and from southern Nyasaland southwards, the species being absent from inland areas through most of Tanganyika, Nyasaland and Northern Rhodesia. Birds of the northern block (*grantii*) have the patterning on the collar and on the breast more restricted (especially in the females) than the southern birds. In birds of the southern block the patterning on the collar is brighter and more extensive and the patterning below extends to the lower breast: birds from the Transvaal, Natal and extreme southern Mozambique (Coguno) have the rest of the underparts fairly heavily vermiculated (*sephaena*), but northwards through Southern Rhodesia the vermiculations become lighter and birds from South West Africa and southern Angola across the continent to southern Nyasaland are appreciably less patterned (*zambesiae*).

OTHER VARIATION

Throughout the range of *F. sephaena* there is considerable local variation in size with equatorial birds on the whole being smaller. Exceptionally small birds are found on the Kenya coast and exceptionally large ones in the Upper Zambezi and Chobe valleys. Among birds without the chestnut streaks on the abdomen there is considerable variation in the amount of vestigial patterning on the abdomen, some having ill-defined whitish streaks and irregular dusky U-patterning. On the whole eastern birds in, and bordering, the hybrid zone tend to be more patterned than western.

In South West Africa some rather greyer birds are found, probably associated with the limestone pans, but the variation is not constant.

EVOLUTION

The peculiar distribution of *F. streptophorus* is the major problem set by the Striated Group. The fact that the eastern and western populations of *streptophorus* are not strongly differentiated and yet the country in between appears totally unsuitable for the species indicates that these are relicts from an era when the group had a wide distribution north of the Congo forest. Being relicts they may not now be in their natural habitat and it can, therefore, be reasonably postulated from the distribution of *sephaena*, that the natural habitat of the Group is in acacia steppe, and that proto-*streptophorus* once occupied this belt from the Sudan westwards,

north of the forest and woodland belts. One thinks usually of these belts as moving north and south with successive climatic fluctuations, but it is possible to visualise that the ridge of higher ground that stretches at about latitude 6°N from the Cameroons eastwards to Uganda may sometimes dislocate regular north-south movement. It seems possible that, following a dry era in which the belt of acacia steppe lay as far south as this ridge, the return of more humid conditions and richer vegetation might come first to the lower country of the Shari basin and Bahr-el-Ghazal to the north of the ridge, leaving temporarily a pocket of dry country on the ridge while the main belts moved north. If proto-*streptophorus* became isolated in this pocket it could be expected that, as conditions became more humid and less and less suitable, it would be driven to the only parts where a tolerably dry habitat could still be found, and one which would be unattractive to the indigenous francolins of the encroaching woodlands. Such refuges were provided in the higher ground at the western and eastern extremes of the previous range.

It is possible that *streptophorus* may yet be found in the country between the Cameroons and Uganda, but if so could be expected only in some patches of sparse vegetation. Since so little divergence is shown by the Cameroon bird it can be postulated that it has been separated from the Uganda population at a comparatively recent date.

The pattern presented by *sephaena* points to at least one unfavourable era in which the species was divided for long enough to allow the streaked and unstreaked types to develop in isolation, almost to the specific level. The present distribution shows how small an extension of woodland towards the coast in Tanganyika would divide the species. In a considerably wetter era with a wide spread of woodland or forest it is likely that the northern populations would be confined to the coastal plain of Somalia while the southern populations might develop on the fringes of the Kalahari. If this was followed by a dry era with a spread of acacia the unstreaked southern populations might spread northwards up the Luangwa valley, through Tanganyika and Kenya along the valleys of the rivers which run westwards to the lakes, and then up the Abyssinian Rift to the Somali highlands.

Meanwhile the streaked northern populations spread southwards, chiefly in the valleys of the rivers flowing to the sea. It is difficult to account for the fact that the two types seem to behave as species in the south but mix and interbreed to a limited extent in the north. It may be that the two came together at a later date in the south when speciation was further advanced, and it is also possible that in northern Tanganyika the sharper change of altitude on the edge of the coastal plain may provide here a barrier that is lacking in Kenya and eastern Somalia (though not in the mountains of (British) Somaliland).

The present gap in distribution between the unstreaked birds of Kenya and northern Tanganyika (*grantii*) and those of the Rhodesias and southern Nyasaland (*zambesiae*) is sufficient to account for the divergence between them.

The scattered distribution of *sephaena* along watercourses in the drier areas would account for much of the local variation in both size and patterning that is exhibited, for such populations would be isolated and might be expected to diverge in periods when there is little suitable vegetation between one river valley and another.

A summary of the evolution postulated is as follows:—

Stage 1. Ancestral stock occupying the acacia belt north, east and south of the central forest and woodland block.

Stage 2. The stock split into two, one, *proto-streptophorus*, in the acacia belt north of the central forest, the other, *proto-sephaena*, in acacia in the eastern districts from Somalia to southern Africa. This split probably taking place in a humid era with a spread of woodland or forest between Uganda and Abyssinia.

Stage 3. *F. sephaena* split into a northern group, probably confined to lowland in Somalia, and a southern group, probably on the borders of the Kalahari. The northern group being the ancestral stock of the birds with streaked abdomens, and the southern group of those with unstreaked abdomens. This split taking place in an even wetter era than Stage 2 with a wide spread of forest and woodland over most of central Africa. *Proto-streptophorus* still isolated south of the Sahara.

Stage 4. (East). A return of arid conditions with increased acacia allows the northern streaked birds to spread down the coast, and the southern, unstreaked birds to spread north up the Luangwa valley, through western Tanganyika and Kenya and the Abyssinian Rift. The two types meet first in the north, and in Somalia they mix and interbreed to a limited extent forming a hybrid zone but with streaked birds always predominant near the coast. Subsequently they meet in northern Tanganyika and later still in southern Nyasaland, but do not interbreed.

Stage 4. (North). In a dry era the acacia belt and *proto-streptophorus* move south to the ridge of high ground from the Cameroons to Uganda and north-western Kenya (Map 6A).

Stage 5. (East). An increase in humidity with a spread of woodland in central Africa cuts off the northern unstreaked birds, *proto-grantii* subsp., from the southern unstreaked birds, *proto-zambesiae/sephaena* subsp.

Stage 5. (North). An increase in humidity, coming first to the low ground of the Shari basin and Bahr-el-Ghazal, north of the ridge, isolates *proto-streptophorus* along the ridge. Increased humidity and competition with indigenous woodland species drive it into refuges at the extremes of its range where more arid conditions persist.

THE RED-WINGED GROUP (MAP 7)

(*F. psilolaemus*, *F. shelleyi*, *F. africanus*,¹ *F. levaillantoides*, *F. levaillantii*, *F. finschi*)

RANGE AND CHARACTERS

This is a very homogeneous group which ranges over most of eastern and southern Africa from Eritrea to the Cape and westwards to Angola. The various species have a complex distribution but are largely allopatric though the ranges of three overlap in the Transvaal. Members of the group are found in a wide variety of habitat and at any altitude, and even individual species are found in varying habitats in different parts of their range.

¹ *F. afer* of Praed & Grant—see appendix.

All birds of the group have "quail-type" plumage on the backs, with a lattice-work pattern of irregular white or buff bars and shaft streaks on a basic colour of mixed black, brown, grey and chestnut: all have the under wing-coverts and part of the wing chestnut (including the South African form *F. africanus*, commonly known as the Greywing, in which the chestnut is reduced): all have a marked facial pattern but this, and the pattern on the underparts, varies in the different forms: all have black bills, usually with a yellowish base, and yellowish legs, the males usually with a single spur. The sexes are alike.

SPECIES AND POTENTIAL SPECIES

The distribution and relationships of the various forms of this group would be easier to discuss if no previous attempt had been made to designate species or subspecies in the East African forms. I cannot agree with any of the classifications made for this group which seem to place too great a reliance on minor morphological characters, particularly the size of the bill, without regard to the ecology of the forms of their likely evolution. The rearrangement I propose I believe to be more realistic in these respects, though I appreciate that conventional nomenclature fails to give more than an inadequate picture, and it is necessary as well to discuss the relationships in some detail. To facilitate the recognition of the species as rearranged they will be discussed under separate headings and I have proposed new common names for each.

F. psilolaemus—The Montane Redwing.

F. psilolaemus comprises the montane populations of Kenya, Uganda and Abyssinia known by Praed & Grant as *F. shelleyi theresae*, *F. s. elgonensis*, *F. afer psilolaemus* and *F. a. ellenbecki*.

All these birds are found in heath and grasslands above 8,000 ft. All have a high proportion of rich chestnut in the wings and differ from other red-winged francolins in having some barring on the tips of the primaries: the underparts are rich buff mottled with chestnut and with some dark brown or black markings: the facial pattern is broken and ill defined. Birds from the Shoa mountains round Addis Ababa (*psilolaemus*) are small with small bills (wing ♂164–174, bill ♂30–34), and have blackish spots on the throat, indistinct black spotting on the upper breast and rather sparse chestnut and blackish patterning on the abdomen. Birds from the Arussi plateau south of the Abyssinian Rift (*ellenbecki*) are slightly larger than *psilolaemus*, darker on the head and back, the lighter markings being greyer: below the spots on the throat and breast are darker and the patterning is stronger and richer in colour. Birds from Mount Kenya and the Aberdares (*theresae*) are large (wing ♂174–191, bill ♂35–38): they have only occasional speckles on the throat but are heavily spotted on the upper breast: they are darker above than Abyssinian birds and the chestnut markings on the abdomen are richer. Birds from Mount Elgon (*elgonensis*) are similar to *theresae* but darker and richer.

F. shelleyi—Shelley's Redwing.

F. shelleyi comprises the forms known by previous authors as *F. s. shelleyi*,

F. s. whytei, *F. afer uluensis*, and *F. a. macarthurii* Van Someren, 1938, but excludes *theresae* and *elgonensis* which were previously ascribed to *shelleyi* (see above).

All the birds included in this assemblage differ from *F. psilolaemus* in having the breast maroon, chestnut and grey, unmarked with black below the necklace and gorget: the remainder of the underparts are patterned all over with black and white, the pattern basically of white spots on a black ground, but the spots frequently merging to form irregular bars. In Kenya and northern Tanganyika birds of this type with rather small bills, white throats, well-defined facial pattern and necklace and rather small patterning on the abdomen are found on hillsides, grassy plateaux, and clearings in montane forest from Mount Kenya southwards to the Crater Highlands and Mount Meru. On Mount Kenya and the Aberdares they are found at lower levels than *F. psilolaemus* keeping below the montane forest. Since they are confined to uplands above 3,000 ft., their distribution is necessarily discontinuous and some divergence is shown by isolated populations, birds of the Loita Plains in south-western Kenya being rather greyer and those of the Chyulu Hills (*macarthurii*) rather darker than birds from central Kenya (*uluensis*).

The most southern representative recorded of this small-billed form is from Mbulu at 4,900 feet in the highlands south of Lake Manyara in northern Tanganyika. Fifty miles south-east at Salanga on the Bereku Ridge at about 5,500 feet a large-billed bird has been collected which has larger, more open, patterning on the abdomen: between the two localities there is lower, rather open country probably unsuitable to these francolins. Birds of the large-billed type are found on the Uganda/Tanganyika borders and at scattered localities through western and southern Tanganyika, Mozambique, southern Nyasaland, southern Northern Rhodesia, Southern Rhodesia the Transvaal and Natal. The small-billed, small-patterned form of Kenya (*uluensis*) and the large-billed, large patterned form of Tanganyika (*shelleyi*) have been regarded as belonging to different species and the proximity of the two in the Mbulu area lends weight to this view. Nevertheless, they seem to have similar ecological requirements and field habits; and, while in the Mbulu area the topography of the country may inhibit interbreeding, there is a bird from Amani, 200 miles to the west, which is intermediate between the two forms in the patterning on the abdomen, though closer to *shelleyi* in bill size, which suggests there may be no intrinsic barrier.

The long-billed *shelleyi* is found in varying habitats throughout its range. In southern Nyasaland, as in northern Tanganyika, it may be found on montane grassland up to 7,000 feet, but it is also found in Nyasaland and Northern Rhodesia in grass under brachystegia or even mopane at low altitudes, though it is nowhere common. In Southern Rhodesia it is common in Mashonaland and the Midlands, in open grass of the plateau, but scarcer westwards in Matabeleland (Smithers *et al.*, 1957: 46). It occurs at least as far south as Pretoria and Legogot, in the Barberton district of the Transvaal, in presumably the same type of country as in Southern Rhodesia, but in Natal is found in acacia country below 2,000 ft. along the foothills of the Drakensburg.

In northern Nyasaland, the south-eastern Congo and northern Northern Rhodesia the species (as proposed) is represented by another long-billed form (like *shelleyi*), but

with a small patterning (like *uluensis*) and which differs from both in having a buff throat with the facial pattern and necklace freckled and indistinct. This form (*whytei*), like *shelleyi*, is found at varying altitudes and in both brachystegia and montane grassland and, though there is no ecological barrier between them and they have been collected from within 40 miles of each other at Lundazi and Mzimba, no intermediates are known (Benson, 1951: 79). Benson tells me that he believes this is more likely to be due to lack of collecting and to the scarcity of both forms, rather than to the existence of any barrier to interbreeding. The situation may be found to be comparable to that between *uluensis* and *shelleyi* in northern Tanganyika but further research is required.

F. africanus (*F. afer*)—the Greywing.

I regard the South African Greywing as a monotypic species, and do not associate any of the northern short-billed forms with it. It differs from *F. shelleyi* in having a white throat flecked with black, the facial pattern obscured by black-and-white freckling, the patterning on the underparts very small, and the rufous in the wing very much reduced. The bill is small as in *uluensis*. It is found in the grasslands of the mountains of the southern Transvaal, Orange Free State and Cape Province, reaching Natal on the high spurs of the Drakensburg. McLachland & Liversidge (1957: 94) show an overlap in the ranges of *F. shelleyi* and *F. africanus* in the southern Transvaal but I cannot substantiate this, the most northerly specimens of *africanus* recorded being from Potchefstroom and Wakkerstroom, 100 miles south of *shelleyi* at Pretoria, and in rather different country.

In Natal Vincent tells me there is a clear altitudinal distinction between them, *africanus* being found above 6,000 ft. and *shelleyi* below 2,000 ft., while the intermediate levels are occupied by a third member of the group, *F. levaillantii*. Furthermore *F. shelleyi* has an earlier breeding season than the other two species, which would contribute to segregation.

It will be appreciated therefore that *africanus* has, in many respects, the same relationship to *shelleyi* in the Transvaal as *shelleyi* has to *whytei* in Northern Rhodesia and to *uluensis* in Tanganyika, in that it appears to be completely allopatric and to exhibit distinct morphological differences. But, whereas there appear to be no ecological barriers between *shelleyi/uluensis* and *shelleyi/whytei* and the morphological differences are slight, there is a distinct ecological barrier between *shelleyi* and *africanus* and morphological differences are greater, representing a greater degree of divergence. This to me is just sufficient to warrant giving *africanus* specific rank.

F. levaillantoides (olim *F. gariepensis*)—Acacia Redwing.

F. levaillantoides comprises all the subspecies of southern Africa usually ascribed to this species and in addition the northern populations known by Praed and Grant as *F. afer stantoni*, *F. a. friedmanni*, *F. a. archeri*, *F. a. lorti* and *F. a. gutturalis*.

It will be seen from the foregoing that I regard the red-winged francolins of the northern and southern acacia steppe as conspecific. They differ from *F. psilolaemus* and from *F. shelleyi* in being paler and less patterned below, lacking on the abdomen

the rich chestnut markings of *psilolaemus* or the black-and-white patterning of *F. shelleyi*, having instead sparse chestnut and blackish flecks or streaks, more common in the northern birds.

In southern Africa they are found in the arid zones from coastal Angola through South West Africa, Bechuanaland, Orange Free State and the Transvaal to the east coast in extreme southern Mozambique, associated, at varying altitudes, with open grassland, hillsides and kopjes, and edges to limestone pans. There are sight records (not included on Map 7) from the Lower Orange River (Winterbottom & Courtenay-Latimer, 1961: 11-12 and *in litt.*). The range of *levaillantoides* overlaps that of *africanus* in the Orange Free State and that of *shelleyi* in the Transvaal. There is little information on their relationship here (perhaps because their numbers have been heavily reduced since the country was settled) but it can be expected that *levaillantoides* would be found at lower altitudes than *africanus*, and in drier areas than *shelleyi*.

In the northern acacia belt the red-winged francolins are found in much the same habitat as southern birds, in sparse grass on rocky hillsides and mountains between about 2,000 and 7,000 feet. In central Abyssinia, where the Acacia Redwing is found in the same areas as the Montane Redwing, it occupies the lower slopes and *F. psilolaemus* the higher (Friedmann, 1930: 112-116).

In northern Abyssinia and Eritrea there is an isolated population (*gutturialis*) found in scrub above 6,000 feet (Smith, 1957: 20). These birds appear to be a link between the acacia species and the Montane Redwing *F. psilolaemus*, for, like the montane bird, they have the facial pattern freckled and ill defined. They also differ from other Acacia Redwings in having the abdomen regularly marked with heavy blackish streaks on the feather centres, though the actual shafts are white, while the flanks are broadly streaked with chestnut. However, in colour and in the distribution of patterning below they seem closer to the Acacia Redwings and are tentatively regarded as conspecific with them.

Otherwise variation in pattern among the Acacia Redwings is slight. All have the facial pattern and necklace well defined, but in birds from southern Angola (*jugularis*) south at least to the Cunene, the black-and-white necklace is enlarged on the breast to a broad gorget. The birds from the Benguela area are exceptionally small, and also rather grey, while Cunene birds are larger and rufous. Throughout both the northern block and other members of the southern blocks there is similar, very marked variation in colour between grey and rufous populations, largely associated with ecology, but there is remarkably little consistent difference between northern and southern birds in spite of the great distance separating them; those from the north have commonly, however, fine dark markings on the abdomen that are usually lacking in those from the south and the abdomens are whiter, less buff. The greyest populations are found in the mountains of eastern (British) Somaliland (*lorti*), in the Kalahari (*kalaharica*—see appendix), and in the Benguela district (as already noted). The most rufous birds are found in the Transvaal and Orange Free State (*levaillantoides*), while in both South West Africa (*pallidior*) and southern Abyssinia and southern Sudan (*archeri*) both rufous and greyish micro-populations are found haphazard (see appendix).

It will be seen that, as far as the northern populations of the red-winged francolins are concerned, the subspecies of the acacia zone could be considered conspecific with *F. shelleyi*, since they are allopatric. However, since in southern Africa *F. levaillantoides* and *F. shelleyi* both occur in the Transvaal, two species must be recognised, and as the northern acacia populations are closer both morphologically and ecologically to the southern acacia birds than to *F. shelleyi*, it seems logical to associate them in the same species.

F. levaillantii—Levaillant's Redwing.

I have made no rearrangement in this species, which is universally recognised as comprising scattered populations from north-western Kenya to the Cape and western Angola and which differs from all other red-winged francolins in having an ochre collar and the sides of face and edges of the throat ochre inside the black-and-white facial pattern. Such populations are found in north-western Kenya, where west of the Rift *F. levaillantii* replaces *F. shelleyi* in grasslands and valleys of the plateaux between 6,000 and 8,000 feet. In Uganda and Ruanda it is found at varying altitudes being common in the lower grasslands west of Lake Victoria (south of Bukobo) and on the plateaux westwards to Lakes Edward and Kivu.

It is absent from most of Tanganyika but reappears on the Njombe and Iringa mountains in the south-west, and on the Nyika Plateau of northern Nyasaland, where it is common above 7,500 feet alongside the rarer *F. shelleyi whytei* (Benson, *in litt.*). Another isolated population is found on the Kibera Plateau in Upemba, southern Congo, at about 6,000 feet (Verheyen, 1953: 256), and scattered populations are found in the grasslands of the Balovale and Mongu districts of north-western Northern Rhodesia westwards through Angola to the Mombolo plateau and the Bailundu highlands. In southern Africa it is found only from the Zoutspansberg southwards through the eastern Transvaal, Natal (between 2,000 and 6,000 feet), Basutoland and the coastal districts of eastern Cape Province, keeping to the moister grasslands and even reed-beds in river valleys. It seems, therefore, in the Transvaal, Natal and Orange Free State, where the four species of Redwing occur, that *F. levaillantii* is associated with the wettest habitat.

The distinctive ochre patterning of the face and throat of *F. levaillantii* has already been noted: it is otherwise most like *F. levaillantoides* but is long-billed and darker and richer in colour, with the black-and-white patterning of the necklace and gorget extending in a complete collar round the hind neck below the ochre collar, and the black-and-white stripes from above the eye, which in *levaillantoides* and *shelleyi* run down the side of the face, in *levaillantii* run behind the head to join at the back. In spite of the wide range and broken distribution there is little variation between the populations but in the populations of southern Africa and of the Nyika plateau these stripes continue down the back of the neck to join the black-and-white collar, while in the western and northern populations the ochre collar is unbroken. The Nyika birds (*crawshayi*) are richer in colour than those of southern Africa (*levaillantii*), with more rufous in the wing, and with more black markings on the abdomen, while the northern birds without the stripe on the hind neck (*kikuyuensis*) are otherwise similar to *crawshayi*.

F. finschi—Finsch's Redwing.

The last of the red-winged species, *F. finschi*, is monotypic. It has a very limited distribution being recorded only from about six localities in western Angola, in a strip about 200 miles long from near Nova Lisboa in the south to Vila Salazar in the north, and again from Brazzaville, in the Congo, 350 miles to the north. On Mount Moco in the Bailundu highlands it was found in the brachystegia woodlands and on the bare upper slopes between 6,500 and 7,000 feet (Hall, 1960a: 408) but the specimen from Vila Salazar (American Museum of Natural History) must have been obtained in very different habitat at not more than 2,000 feet, and at Brazzaville Malbrandt and Maclatchy (1949: 142) found it in grassland with neighbouring woods in which the birds took refuge.

It is possible that the different habitats of *F. finschi* may be partly due to competition with *F. levaillantii*, which occupies grasslands in the southern part of the range, but is not found north of the Mombolo plateau.

F. finschi differs from other red-winged francolins in lacking any black-and-white patterning on the face and neck and having the breast grey: it is closest to *F. levaillantii* in having a long bill and the sides of the face and border of the throat ochre, but in *F. finschi* the ochre is not so extensive on the hind neck: the abdomen is a mixture of buff and pale chestnut.

OTHER VARIATION

Considerable individual variation is to be expected in any birds as intricately patterned as the red-winged francolins and is found in all species. There is some local variation, usually in an increase or reduction of rufous and grey in the plumage, associated with ecology. This, as noted, is particularly marked in *F. levaillantoides*, but since the problems it raises are largely nomenclatorial it is discussed fully in Appendix 2.

EVOLUTION

The complex pattern displayed by the seven species of the Red-winged Group is not easy to interpret but I believe may be partly explained by comparison with a rainfall map (Map 7A). From this it will be seen that the range of *F. levaillantoides* falls largely in the parts where the rainfall is below 20 inches in the year, the range of *F. shelleyi* falls between the 20–40 inch isohyets, the range of *F. levaillantii* falls between the 40–60 inch isohyets, while the range of *F. finschi* coincides remarkably with the only two patches south of the Congo rainbelt where there is over 60 inches in the year. Thus a slight increase or decrease of rainfall may be expected to favour the spread of one species at the expense of others. The discontinuous distribution of all species, and the scarcity of red-winged francolins in so many parts of their range, suggests that the present cannot be regarded as a favourable era for any members. This might be due to competition with other groups, but if so it could be expected that *F. levaillantoides* would be more common in the Kalahari, where there is no competition. From the association of so many members of the group with mountains I believe that a colder era would be more favourable to the group as a whole, and it was in some such era or eras, with fluctuations in rainfall, that

continuity in the ranges of the various species was achieved. Conversely warmer eras could be regarded as least favourable and ones most likely to produce isolated populations in which speciation developed.

Even with this hypothesis as a basis a good many interpretations of the pattern present themselves which are largely dependent on which species one believes are most closely related. The following sequences are put forward tentatively on the premise that plumage pattern is the best guide to relationship. I can offer no explanation of the variation in bill size in terms of evolution and relationship but it is worth noting that in this group it is the species and, in *shelleyi*, the subspecies, associated with the higher rainfall areas that have the long bills. The length may perhaps be correlated with the hardness of the ground in which the birds search for food.

The distinctive patterning on the abdomens of *F. africanus* and *F. shelleyi* suggests that their common ancestor split at an early date from the rest of the group. The present distribution suggests they developed in the south; later spreading north to Kenya in a favourable era; later splitting into two blocks, proto-*africanus* and proto-*shelleyi*; later proto-*shelleyi* splitting into three from which the subspecies *shelleyi*, *whytei* and *uluensis* developed. A favourable era must have followed in which their distribution was continuous over the present range.

The species with relatively unpatterned abdomens may have originated in the north. A warm era could be expected to drive members of this block to the extreme north of the range, and also to high altitudes: it can be postulated that proto-*psilolaemus* developed in such an era to specific status and became adapted to montane conditions: later in a favourable era other members of the northern block spread south and west as far as Angola and the lower Congo. A subsequent unfavourable era isolated first proto-*finschi* in the Angola mountains, then proto-*levaillantii* in the mountains of central Africa, and proto-*levaillantoides* in Abyssinia, Somaliland and Eritrea: in isolation each became adapted to different degrees of humidity: subsequent fluctuations in rainfall allow first proto-*levaillantoides* to spread widely through the continent and then proto-*levaillantii*. The small degree of divergence shown between the isolated populations of both species (with the exceptions of *F. levaillantoides gutturalis* in Eritrea which perhaps was isolated earliest) suggests that these dry and wet cold spells were comparatively recent.

A summary of the evolution postulated is as follows:—

Stage 1. The group widespread in eastern Africa in a cold era.

Stage 2. The group split into a northern and southern block.

Stage 3. The southern block spreads north, at least to Tanganyika, and the northern block south to Kenya (Map 7B).

Stage 4. Warm and unfavourable, both blocks split into two: in the south proto-*africanus* isolated in the mountains of South Africa, proto-*shelleyi* possibly in the mountains of Nyasaland: in the north proto-*psilolaemus* isolated at high altitude, possibly on Mount Kenya or Elgon, and the ancestral stock of the other species isolated in the extreme north.

Stage 5. Favourable. Proto-*shelleyi* spreads, possibly to the limits of its present

range. Members of the northern blocks (with unpatterned abdomens) spread south and west to Angola.

Stage 6. Unfavourable. Proto-*finschi* isolated first in Angola: proto-*levaillantii* isolated next in some mountains of central Africa not occupied by proto-*shelleyi*, while proto-*levaillantoides* is cut off in the north. Each becomes adapted to different requirements of humidity.

Stage 7. In a long cold era favourable to the group as a whole, fluctuations in rainfall and temperature favour each species in turn. In some unusually cold spell proto-*psilolaemus* spreads to cover a large part of Abyssinia and Kenya but is later split into isolated populations in the highest mountains. Proto-*shelleyi* following a favourable era is split into three, from which the subspecies *shelleyi*, *whytei* and *uluensis* develop almost to specific status. An unfavourable spell in the north isolates proto-*gutturalis* in Eritrea from the main body of proto-*levaillantoides*: in a subsequent dry spell (during which the acacia spreads to link the northern and southern belts) proto-*levaillantoides* spreads south to Bechuanaland. In a wet spell proto-*levaillantii* spreads at the expense of *shelleyi* and *levaillantoides*, and proto-*finschi* spreads: where the two come together *finschi* is pushed into the mountains.

Stage 8. The present. Too warm to be favourable to any members of the group, the ranges of all species being discontinuous and the birds uncommon in most areas.

THE RED-TAILED GROUP (MAP 8)

(*F. coqui*, *F. albogularis*, *F. schlegelii*)

RANGE AND CHARACTERS

This is a group of small francolins (wing under 150 mm.) which ranges from Senegal to the Sudan, and from central Kenya west to the central Congo and Angola, and south to the Transvaal and Natal: there is an isolated population in the Rift of Abyssinia. Members of the group are found in woodland, savanna and steppe and, in parts of the range, often on the same ground as other francolins, which suggests that their smaller size may make them non-competitive. The group is formed of three species which are allopatric except in the southern Congo and eastern Angola where isolated populations of *albogularis* are found within the range of *coqui*.

All members of the group have a considerable amount of ochre on the sides of the face, spreading as an ill-defined collar on the hind neck: the crown is plain brown or chestnut, contrasting with the back which has a quail-type pattern (except in the females of *schlegelii* in which the striations and cross bars are reduced to a minimum), varying in colour from grey and black to vinous rufous: in the redder birds the rufous in the tail is conspicuous but in some of the greyer forms is no more than a pinkish wash on the outer feathers: the underparts are variable but all birds have a white or buff throat contrasting with the breast: all have black bills with some yellow at the base and yellow legs: the males have a single spur.

SPECIES AND POTENTIAL SPECIES

F. coqui is the most widespread of the three species which comprise the group. It is found in short grass in brachystegia woodland from southern Uganda and northern Tanganyika, southwards to the Rhodesias and westwards to Brazzaville and the edge of the Angola escarpment, but is absent from mountains and from the drier acacia steppe of Tanganyika. South of the brachystegia belt it is found in the acacia savanna skirting the Kalahari, from northern South West Africa to the Transvaal, and in the coastal districts of Natal. Scattered populations in Kenya, southern Abyssinia and the Harar area are also found in acacia (Benson, 1945: 390) finding it common around Yavello and Mega in "open short-grassed country with scattered low thorn bushes at 4,000–4,500 feet".

In West Africa there is a population in the acacia belt of Senegal, the Upper Volta and northern Nigeria that is isolated by 1,000 miles (and the Lower Guinea forest) from the Brazzaville birds, and by nearly 2,000 miles from the Abyssinian birds. In this area *coqui* is found commonly in cultivations, often alongside *F. bicalcaratus* (Blasdale: unpublished). However, it seems that at Potiskum, 150 miles east of Kano in northern Nigeria, *coqui* is replaced abruptly by *F. clappertoni* which occupies the acacia belt eastwards to Abyssinia (Hollis: unpublished). In Abyssinia *clappertoni* occupies the northern and western areas to the centre of the Rift but is replaced by *coqui* in the Harar area in the east and in the Mega/Yavello area of the south.

In *coqui* the quail-type patterning on the back is very consistent and well defined, though the basic colour, and the colour of the head, vary from grey to brown or rufous in different populations. The sexes differ, the males having the sides of the face and throat ochre or light buff without a black eye-stripe or necklace, the females having the sides of the face similar in colour to the males but the throat whiter and having a black necklace and a black eye-stripe that continues as a black line down the sides of the face. The males also have the breast barred while in the females the barring is replaced or overlaid by a pink or grey wash.

There is little significant geographical variation in birds of the southern part of the range, from Angola, the Congo, central Tanganyika and coastal Kenya south to South Africa (*coqui*). All have grey wings and barred abdomens (though the degree of barring is variable) and females have a pink wash on the breast. In the Abyssinian population (*maharao*) the wings are rufous and both sexes have light narrow barring from breast to abdomen, the females having only a faint wash of pinkish grey over the barring on the breast. The isolated West African population (*spinetorum*) also has rufous wings, but is pale above, washed with pink, and there is no barring on the abdomen in either sex: the breast of male is broadly barred and that of the female plain and pinkish-grey. In Uganda, Kenya and Tanganyika the pattern of variation is confused. East of the Rift in Kenya, south to the Arusha area of Tanganyika, there is a population (*thikae*, Grant & Praed, 1934) known only from a few specimens, which shows some approach to the Abyssinian birds in having rufous wings, light barring, and vestigial barring on the breasts of the females, but with no barring on the abdomens in either sex. From the Rift westwards to the eastern shores of Lake Victoria the birds (*hubbardi*) are similar to both the West

African *spinetorum* and the eastern *thikae* in having plain abdomens but the wings are grey like the southern *coqui*, the breasts of the females are plain and grey, and the whole upperparts are rather dark and grey. Birds from west of Lake Victoria (*ruahdae*) are close to the southern *coqui*, but have the black barring broader and more widely spaced. These birds intergrade with *hubbardi* in the Tabora area.

The second species in the group, *F. albogularis*, has a scattered distribution. There is a population in the Gambia, found mostly on the edges of cultivation, but it is rare (Hopkinson, 1923: 129). Other populations are found on the coastal plain near Accra and in the hinterland of Ghana, eastwards through Nigeria to Garoua in the (French) Cameroons. Field notes on these birds are scarce and somewhat contradictory, Serle (1957: 389) finding them common in "the open savannas and rolling hill country" of Eastern Nigeria, whereas Blasdale tells me that further north he has found them only in thick woodland where there is abundant *Isoberlinia doka*. Most localities from which they have been collected lie within the woodland belt (Map 11, Type 17) but Garoua lies within the acacia savanna belt (Map 11, 20) and the specimen was obtained in "open, sandy, sparsely-treed country" (Good, 1952: 67).

F. albogularis is absent from the woodland and savanna belt north of the Congo forest (where *F. schlegelii* is found) but reappears again 1,500 miles away in the south-eastern Congo on the plateaux of Marungu and Kibara, in the Upemba National Park, on the plains of the Balovale district of Northern Rhodesia, and on the treeless dambos of the Zambezi/Congo watershed in eastern Angola.

Above *F. albogularis* is very like *F. coqui* but the quail-type patterning is less well defined in the females, the shaft streaks and barring being narrower: the wings are more rufous (similar in this respect to the east Kenya population, *thikae*). As in *coqui* the females have a black facial pattern and necklace, but it is ill defined, and the males have none, though they differ from *coqui* in having a white throat contrasting with the ochre cheeks, as in the females. In the rest of the underparts the males of *albogularis* are quite distinct from any form of *coqui* being chestnut on the breast with ochre shaft streaks and rich ochre on the abdomen, lacking any dark barring. The females on the other hand are barred, in greater or lesser degree according to the population, with a faint wash of pink or rufous on the breast, and resemble closely the females of the Abyssinian and east Kenya populations of *coqui*. The population of *albogularis* in which the females are least patterned is in the Gambia (nominate *albogularis*) the barring being light and restricted to the breast and flanks (though varying individually). In birds from Ghana to the Cameroons (*buckleyi*) the barring is generally heavier, usually with only the centre of the abdomen unpatterned. Birds of both sexes from the populations south of the Congo forest are slightly larger and more richly coloured than those from West Africa and in the females of the south-east Congo (*dewittei*) the barring is heavier but no more extensive than in *buckleyi*: the darkest birds with the most heavily barred females are found in eastern Angola and possibly the Balovale district (*meinertzhageni* White, 1944—see appendix).

The third species of the group, *F. schlegelii*, has been considered by Chapin and Peters to be a subspecies of *F. coqui*. I believe it is distinct enough to warrant

specific status and furthermore is closer in several respects to *F. albogularis*.

It is a rare bird, found scattered through the woodland and savanna belt from the eastern Cameroons to the western Bahr-el-Ghazal. From what Cave tells me it seems to be more consistently a woodland bird than *albogularis* and he has the impression that it is found in rather denser woodland than the sympatric *F. icterorhynchus* of the Vermiculated Group, especially where there is *Isoberlinia doka*.

Above *schlegelii* is closer to *albogularis* than *coqui*, though the quail type patterning is much reduced and the sexual dimorphism is more pronounced, the males having broad white shaft streaks but few transverse bars while the females are almost unpatterned: both sexes have a soft vinous wash. Below the male of *schlegelii* is like that of southern races of *coqui*, with ochre sides of the face and throat and narrow black and white barring over the breast and abdomen: the female resembles the male on the head and throat but has the breast grey, patterned with cream triangular marks at the base of the feathers, the flanks sparsely barred, and the centre of the abdomen plain cream.

OTHER VARIATION

In the southern populations of *F. coqui* there is local and ecological variation in size and colour; exceptionally small birds are found in coastal Kenya and Natal; grey, pale birds in Bechuanaland (*vernayi*) and pale, rather pinkish birds in South West Africa (*hoeschianus* Stresemann, 1937): other exceptionally grey birds occur in southern Mozambique (Coguno) and may be expected locally in dry conditions, while pockets of more richly coloured birds are associated with richer vegetation. There is otherwise little variation between birds from Natal and the Transvaal north to coastal Kenya and west to Northern Rhodesia, except in the extreme west: here and in Angola the birds are consistently less rufous and the bars on the underparts are narrower and rather closer together (*angolensis*). Birds from Kasai and western Katanga (*kasaicus* White, 1945) are similar to *coqui* above and *angolensis* below: they intergrade with *coqui* in the eastern Katanga.

In *F. albogularis* of West Africa individual variation in patterning has already been noted. Serle (1957: 388) also found the general colour individually variable between rufous and grey, though there seems a tendency for the coastal population of Accra to be greyer than inland birds.

Individual variation is also found in *F. schlegelii* especially in the females (see Traylor, 1960b: 86).

EVOLUTION

The most striking features of the pattern presented by the Red-tailed Group are the enormous distances separating the north-western and south-eastern subspecies of both *F. albogularis* and *F. coqui*: also, in *F. coqui*, the complexity of variation in East Africa in contrast to the uniformity of southern birds. I feel confident that the discontinuous range of *F. albogularis* is largely attributable to the presence of *F. schlegelii* in the intervening segment of the same vegetational belt, and suggest that the ancestral stock of the two species once had a continuous distribution in the savanna and woodland encircling the Congo forest. To account for the split into two species I suggest this era was followed by a very dry period in which the forest was divided into a western and eastern block each encircled by woodland and separated by a corridor of acacia linking the northern and southern

acacia belts. It can reasonably be postulated that proto-*albogularis* developed in the belt round the western forest and proto-*schlegelii* in the belt round the eastern forest (Map 8B). When the two forest blocks rejoined with a return of humid conditions and the surrounding belts became one again, the central segment of the belt was occupied by proto-*schlegelii* and the western and southern segments by proto-*albogularis*.

It is more difficult to interpret the pattern of *F. coqui* but a logical sequence can be found which will fit into that postulated for the other species. Proto-*coqui* may have been separated from the ancestral stock of the other two species at a time of spread of montane forest and developed in the east while proto-*albogularis*/*schlegelii* developed in the north. With the retreat of the forest proto-*coqui* spread south and west chiefly in acacia savanna. In an unfavourable spell, either too wet or too dry, proto-*maharao* in Abyssinia was isolated. In the very dry era postulated above, in which there was a corridor of acacia in the central Congo, proto-*coqui* could have spread into the northern acacia savanna belt. Subsequently with a return of humid conditions the northern population would be cut off from the southern by woodland and forest. The southern populations nearest the Equator prove adaptable so that, with the return of woodland and savanna and the indigenous *albogularis* to the southern Congo and Angola, *coqui* competes successfully, occupying the woodlands and *albogularis* the more open grasslands and plateaux.

Meanwhile the isolated northern population diverges from southern birds, developing the distinctive unpatterned abdomen in both sexes, and spreads through the northern acacia belt west to Senegal and east through the Sudan to Kenya and Uganda. Here it encounters both the Abyssinian *maharao* and the southern *coqui*. The characters of the present populations of Kenya (*hubbardi* and *thikae*) and of southern Uganda (*ruahdae*) suggest that some interbreeding took place at some period.

The present appears to be favourable to the Vermiculated Group in the north, at the expense of the Red-tailed Group. In the immediate past it seems that *F. clappertoni* has spread west through the acacia belt in the Sudan, eliminating *coqui* between the Nile Valley and northern Nigeria. In the woodland and savanna belt *F. bicalcaratus* flourishes in the west and *F. icterorhynchus* in the east, and competition with these two may account for the scarcity and discontinuous distribution of *albogularis* and *schlegelii*. However, in West Africa *coqui*, though apparently unable to compete with *clappertoni*, is yet able to live on the same ground as *bicalcaratus* on the southern fringe of the acacia belt. The populations of *coqui* in eastern and southern Africa also seem able to co-exist on the same ground as other francolins.

A summary of the evolution postulated is as follows:—

Stage 1. The group develops in savanna, perhaps in north-eastern Africa.

Stage 2. An unfavourable era, possibly a spread of montane forest. The group splits into two with proto-*coqui* isolated in the east and proto-*albogularis*/*schlegelii* to the north of the forest.

Stage 3. More favourable. Proto-*coqui* spreads south and west in rather dry

savanna, mostly acacia. *Proto-albogularis/schlegelii* spreads in the wetter savanna and woodland encircling the lowland forest of the Congo Basin (Map 8A).

Stage 4. A very dry era. The Congo forest is divided into a western and eastern block, each surrounded by its own woodland and savanna belt, with a corridor of acacia between. *Proto-albogularis* develops in the belt surrounding the western block of forest, *proto-schlegelii* in the belt surrounding the eastern block. *Proto-coqui* spreads through the acacia corridor into the northern acacia belt. In an unfavourable period in the north-east *proto-maharao* becomes isolated (Map 8B).

Stage 5. More humid. The two blocks of forest rejoin and the two savanna belts become one again, the eastern segment being occupied by *proto-schlegelii* and the western and southern segments by *proto-albogularis*. In the southern segment, as woodland and savanna return to districts previously acacia, *proto-coqui* is not pushed out but becomes adapted to woodland and competes successfully with *proto-albogularis* which takes to the more open grasslands. In the north *proto-spinetorum* subsp. spreads west to Senegal and east to Abyssinia and Kenya and diverges from the southern birds. There is limited interbreeding where the northern birds re-encounter other members of the species in the east.

Stage 6. Favourable for the Vermiculated Group, especially in the north. *F. clappertoni* spreads, eliminating *F. coqui* from the acacia belt in the Nile Valley and Sudan westwards to northern Nigeria. In the woodland and savanna belt *F. bicalcaratus* and *F. icterorhynchus* flourish at the expense of *F. albogularis* and *F. schlegelii*. In the south *F. coqui* co-exists more successfully with francolins of other groups.

SPECIES NOT INCLUDED IN ANY GROUP (MAPS 9 & 10)

Francolinus lathamii

F. lathamii is a forest francolin ranging from Sierra Leone to western Uganda and the southern Sudan.

It appears at first sight quite unlike any other African francolin (closer, except in size, to *F. francolinus* of Asia), being, in the male, largely black below with regular white spots, in the female brown with irregular white spots, the throat black and face patterned, the upper parts mottled rufous and brown with some white streaks on the mantle, the bill black, finer than in other francolins. However, comparison of a pair of *lathamii* with a pair of *schlegelii* suggests that *lathamii* may be more closely related to the Red-tailed Group than to any other francolin. It will be seen that the pattern and the colouring on the upper parts are basically the same, though *lathamii*, as would be expected in a forest bird, is darker and more mottled. Below the patterning of the females has some similarity in the irregular, rather triangular shaped spots: while the spotted male of *lathamii* looks very different from the black-and-white barred male of *schlegelii*, this may not be a very significant difference for in odd abdomen feathers of several *lathamii* the spots are less regular and merge as vestigial bars. The chief differences in fact lie in the shape of the bill and the pattern of the face and throat. Furthermore the first plumage of *lathamii* chicks is very similar to the plain vinous mantle of the female *schlegelii*.

While being confident that there are affinities between *lathamii* and *schlegelii* I am not prepared to guess at what period in history proto-*lathamii* became isolated and adapted to forest. The likeness to one particular species in the Red-tailed Group suggests that its isolation could have been subsequent to the emergence of species within the group, the adaptation to such different habitat accelerating divergence. On the other hand *F. schlegelii* is the species of the Red-tailed Group that lives in the thickest woodlands and, if proto-*lathamii* had broken from the ancestral stock of the Red-tailed Group before the three species had diverged, the similarities between *lathamii* and *schlegelii* might be due to convergence. For this reason, and with regard to both its morphological and ecological distinctions, I feel it best to treat *lathamii* independently.

It will be seen that I am not prepared to regard the black-and-white spotting in the males of *lathamii* as indicative of relationship with *F. francolinus*. It has been amply demonstrated in the discussion on groups that the pattern of the underparts is of less significance than size and the pattern above, and while it is interesting that such a striking pattern is repeated in the genus in two such different birds, it cannot be relevant to the grouping of species.

From the distribution plotted on Map 9 it would appear that there is a wide gap between the populations of the eastern and western Congo, but this is more likely to be due to lack of collecting in the central area than to a genuine break. There is little geographical variation, in the males of eastern birds (*schubotzi*) the black-and-white pattern extends further down the abdomen, and the females have the cheeks more rufous than grey, but there is considerable individual variation.

Francolinus nahani

This little francolin is confined to the heaviest forests of the north-eastern Congo and Uganda. It is a distinctive bird, predominantly dark brown or blackish, with white streaks on the underparts and some white spots on the wing-coverts and flanks. The bill is black at the tip and crimson at the base; there is a patch of crimson bare skin round the eye; the legs are crimson, and without spurs in either sex.

It is difficult to assess its affinities with the other francolins. Superficially it appears closest to *F. lathamii* in its small size, general dark coloration and suggestion of spotting, and they occupy the same type of habitat. On the other hand the similarities are in those characters that are to be expected in forest birds, and could well be due to convergence, and the fact that *F. nahani* in the whole of its range is sympatric with *F. lathamii*, without apparently being ecologically segregated, does not suggest close relationship. I would suggest very tentatively that *F. nahani* may have broken off at a remote period from the ancestral stock of the Scaly Group (in the same way as I have suggested that *lathamii* may have broken off from the Red-tailed Group), and become adapted to heavy forest instead of the forest clearings. I suggest this because *nahani*, although much smaller, seems to have some characters in common with the Scaly Group as a whole and with each of the three individual species. In both *nahani* and all species of the group the sexes are alike, and the legs are red: *nahani* is like *F. squamatus* above, having an unpatterned head and

vermiculated back; it is like *F. achantensis* in the white streaking below; and like *F. griseostriatus* in the crimson base to the bill. Furthermore in all species of the Scaly Group there is a small area of bare skin below and behind the eye, though this is not brightly coloured and usually overlooked.

Chapin considered the absence of spurs to be a generic character and proposed the monotypic genus *Acentrortyx* for *F. nahani*, but the fact that *F. pictus* in India is also without spurs, but yet is so closely related to *F. francolinus* as to hybridise, demonstrates that this character is not necessarily significant. I see no other reason for regarding *F. nahani* as generically distinct.

F. pondicerianus

F. pondicerianus is the smallest of the Asiatic Francolins and is widespread from the shores of the Gulf of Oman eastwards through the plains of India and the dry north-western districts of Ceylon, living in grassland or scrub. It appears to have some affinities with both the Red-tailed and the Striated Groups of Africa and in colour and pattern is closest to *F. coqui*, in particular to the geographically nearest form *F. c. maharao* of Abyssinia. It has "quail-type" plumage on the back, but is duller than *coqui*, with broader transverse white bars and narrower shaft streaks, and with chestnut markings on a grey or buffish ground: the underparts are whitish, irregularly barred with very fine blackish bars: the throat is buff surrounded by a blackish necklace, which is smaller than that found in the females of *coqui* and starts from the chin and not the sides of the bill. In other respects it is closer to the Striated Group (*F. sephaena* and *F. streptophorus*) than to the Red-tailed Group, having a longer and more graduated tail (the tail more than half the length of the wing), and stronger (though not necessarily longer) legs and larger feet, the legs being reddish as in *F. sephaena*. The bill is distinct from either group being brownish in colour and heavier in front of the nostrils. The tail in colour combines characters of both groups being reddish at the base but otherwise largely blackish.

The affinities with two of the African Groups suggest that the ancestral stock of *F. pondicerianus* was isolated from the African stock before the Red-tailed and Striated Groups had diverged and for this reason I have discussed it independently. It seems that, while the African stock underwent many vicissitudes of climate with consequent isolating and regrouping of populations resulting in speciation, the Indian stock had a comparatively tranquil history for in *pondicerianus* there is little variation, and that mostly clinal and ecological: birds from the dry districts of Persia and Baluchistan, east to the western Punjab (*mecranensis*), are the greyest and palest, and those from southern India (*pondicerianus*) the darkest and least grey with the greatest amount of chestnut markings. Those from northern and central India (*interpositus*) are intermediate. Ceylon birds (*ceylonensis* Whistler, 1941) are greyer than either *pondicerianus* or *interpositus* but darker than *mecranensis*.

F. gularis

F. gularis is the swamp francolin of India, being confined to reeds and marshes in the plains of the Ganges, Brahmaputra and their tributaries from central Uttar

Pradesh eastwards into Assam. It is a large francolin, comparable in size and general proportions to the largest member of *F. francolinus*, but with rather a shorter bill and larger feet (as would be expected in a marsh bird). It is, however, quite different in colour and pattern being predominantly a brown and white bird, with a barred back, streaked underparts and a rufous throat, wings and tail. The sexes are alike.

Proto-gularis seems likely to have become isolated from other francolins in a dry period and taken refuge in river valleys, becoming adapted to these conditions. The dry era postulated may even have occurred before the link between the Asian and African francolins was broken since the differences from other francolins shown by *F. gularis*, both in ecology and morphology, suggests divergence over a long period.

CONCLUSIONS

THE GROUPS

The chief lesson to be learnt from comparison of the relationships between the members of each group re-emphasises the difficulty of assessing from morphological characters the level of speciation which any form has attained. This is brought home most forcibly by finding that such dissimilar birds as *cranchii* and *afer* in the Bare-throated Group will interbreed freely, while the three Redwings in the Transvaal *shellei*, *levaillantoides*, and *levaillantii*, which look more alike, are able, on account of ecological divergence, to live in a small area without interbreeding.

It seems that a relatively slight ecological divergence among the francolins may be effective against interbreeding because their sedentary habits and specialised choice of habitat make them reluctant to move out of their selected type of vegetation. These same habits allow also for comparatively small barriers to act as isolating factors between two populations that are not necessarily ecologically divergent. Two instances have been given where rivers appear to form such a barrier, the Niger between *ahantensis* and *squamatus* of the Scaly Group and the lower Zambezi between *natalensis* and *hildebrandti* of the Vermiculated Group. In the Red-winged Group fifty miles of unsuitable country in Tanganyika between *F. s. shellei* at Salanga and *F. s. uluensis* at Mbula serves as barrier to interbreeding between them.

The difficulty of designating in these circumstances which members of groups should be called species and which subspecies was discussed at the start of the paper, for the status of most lies somewhere between the two. This should be borne in mind in the subsequent discussion on evolution, for these "species", which are allopatric members of superspecies, for the most part appear to have attained a level of speciation far below that of those species which are able to live with each other in full sympatry.

EVOLUTION

The stages of evolution postulated for each group have been based on what seem to me to be the simplest and most likely interpretations of the patterns shown, and they represent the minimum number of stages which can be envisaged to produce

such a pattern. They represent a sequence rather than a time-table of change and as such could, in theory, be spread over any number of years. However, there is evidence from the distribution of many montane plants and trees, as well as birds, which shows that there have been periods in which montane forest has spread over vast areas of Africa, linking up the present isolated patches in the Cameroons, Angola, East Africa, Abyssinia, Nyasaland and South Africa, descending as low as 2,000 ft. (see Map 3A). At the same time (by inference a wet era) there would be extensive lowland forest below that level. This would have the effect of reducing the refuges for grassland and woodland species to comparatively small areas isolated from each other by forests. Such conditions would not only be catastrophic for many species but would obliterate any traces of the pattern of distribution and evolution prior to that period. Thus, although such a spread of forest may have occurred during any extensive cold wet era, it follows that, if the stages of evolution I have suggested are accepted, the conclusion cannot be evaded that they have been accomplished since the *last* spread. This conclusion carries with it implications on the rate of speciation which need to be examined closely.

In the course of these stages I have suggested that twelve species of francolins (the ancestral stock of the eight groups and the four independent species) have increased to forty-one, all the new species being members of superspecies. The accompanying dendrogram (Fig. 2) summarises the relationship postulated of the



FIG. 2. Dendrogram showing the relationship postulated of the various groups and species, and their date of origin in respect to the last major spread of montane forest.

various groups and species to each other and their date of origin in respect of this last spread. Unfortunately no date can be given yet to this last spread of forest, and there is indeed still uncertainty on the date of onset of the Last Glaciation, opinions varying between 100,000 and 50,000 years ago. Authorities, however, agree that it ended about 18,000 years ago and that there have been at least four glaciations in the course of the Pleistocene. I am suggesting therefore that these changes have taken place in the comparatively short period of the Late Pleistocene (i.e. about the last 100,000 years).

If we accept that *Francolinus* may (among other modern genera of birds) have originated in the Oligocene (approximately forty to thirty million years ago) (Van Tyne & Berger 1959: 6-17) and has taken all the time prior to the last glaciation to divide into twelve species, it seems that I am postulating an incredible acceleration in the rate of increase of species. But this is not so, for, as stated, the concept of periodic spreads of forest over vast areas of Africa is inseparable from the acceptance of a high casualty rate among the non-forest species at that period. If, for instance, the present was followed by a cold, wet era that brought with it a wide spread of forest, it is highly unlikely that any of the less successful non-forest species of tropical Africa would survive (e.g. *rufopictus*, *streptophorus*, *finschii*, *albogularis*, *schlegelii*).

Competition between members of different groups in the limited refuges left would eliminate several of the apparently successful species as well (just as *F. clappertoni* appears to have eliminated *F. coqui* from the Sudan), while members of the same group, forced into unprecedented proximity, would probably interbreed freely. Thus the total number of African species could again be reduced to few (if any) more than the nine which survived the previous forest spread. These would be the ancestors of future groups.

Thus while I believe the number of members in any group may fluctuate widely with successive glacial and inter-glacial eras it seems that any increase in the number of groups and independent species would be very slow and not incompatible with the rate of evolution since the inception of the genus.

It could also be suggested that any further increase is unlikely in this figure, which represents the number of birds which have reached a sufficiently high level of speciation to be able to live sympatrically without interbreeding, for it is evident that only a limited number of such birds can be supported in any given area. In birds like the francolins, in which two species are rarely found actually on the same ground, this limit is governed largely by the number of alternative types of habitat, and the unequal distribution of the groups in tropical Africa gives some reason to suppose that this limit may have been reached.

Disregarding the Montane Group, with its extremely specialised ecology, it will be seen that, apart from a relict population of the Striated Group, only three groups, the Scaly, Vermiculated and Red-tailed, are fully represented in the north-western section (from West Africa to the Sudan and Uganda). There is little overlap between the ranges of these groups and where two do occur together one is thriving at the expense of the other. Furthermore over a vast area it appears that members of the most successful group, the Vermiculated, have totally driven out representatives of

other groups, namely the red-tailed *F. coqui* from Lake Chad to the Nile, and the striated *F. streptophorus* between the Cameroons and Uganda. This north-western section is relatively flat with monotonous vegetation, and no very clear-cut divisions between the vegetation belts: the east and south on the other hand, from Abyssinia to South Africa and Angola, is more mountainous in many parts with more varied vegetation, and here no less than six groups are sympatric or partly sympatric. In this section of Africa I have suggested certain instances in which the range of one group has been restricted by competition with another, but it is also evident that several special may thrive in a small area.

I am not competent to discuss the situation in Asia where the development and status of the francolins must be dependent on those of the numerous other genera of gamebirds which I have not studied, but it seems unlikely that there is much room for an increased number of full species.

In arguing that the members of groups may have developed to the level of members of superspecies within the Late Pleistocene I am conscious that this is postulating a more rapid rate of speciation than is usually accepted, though Rand (1951: 567) has suggested that some of the forest subspecies of West Africa may have evolved in the last 12,000 years, while Moreau (1930) gives examples of Egyptian subspecies which have probably evolved in 5,000 years. However, some weight is added to my argument by the evidence collected by Moreau on the climatic fluctuations that have taken place in this period (Appendix 1), which shows that there has been sufficient variation in both temperature and humidity to bring about the wide redistributions of the montane and lowland forest, woodland, savanna and steppe that would be necessary to the different stages proposed. Furthermore, it shows that all the vegetational changes postulated in the evolutionary sequences in the groups (which were founded entirely on the evidence of the birds alone) did, or could, take place, though it is not always easy to satisfy the sequence.

To support some of the major changes which I have envisaged, he has shown, for instance, that there have been very dry periods prior to 10,000 years ago in Angola and Katanga (at least) which, if they prevailed elsewhere, could have been sufficient to connect the northern and southern acacia belts in the way postulated in the evolutionary sequences of the Bare-throated, Striated and Red-winged Groups. He gives corroboratory evidence for the existence of such a dry corridor at some period in Tanganyika, and Benson and White (in press) suggest this corridor may have been through the Luangwa and Rukwa valleys, and they list many species of birds and mammals whose present distribution has led them to this conclusion.

Moreau shows also that there was a period (undated) at which Lake Chad was 600 miles long, probably with forest at the southern end joining the main Congo forest, so forming a barrier between eastern and western woodland or grassland species, such as was postulated in the Vermiculated Group to split proto-*bicalcaratus* from proto-*icterorhynchus*. He quotes too a record that suggests there was probably lowland forest at Oldowai in northern Tanganyika in the early Pleistocene where there is now acacia steppe. Though this dating can hardly be correlated with the spread of lowland forest envisaged in the later stages of the evolutionary sequence of the Scaly Group, it suggests that such a spread has taken place once and could

therefore be repeated in similar climatic conditions:—perhaps achieved in even one of the recent minor pluvials in East Africa (less than 35,000 years ago).

Similarly he says that late in the Middle Pleistocene there is believed to have been a dry period when the Congo forest was reduced to strips in the east and west (and possibly also on the northern rim) and that there was acacia in the country between. This makes the sequence of evolution postulated for the Red-tailed Group less improbable than it seemed when I first proposed it (before I had seen Moreau's paper), though this sequence remains the most difficult to correlate with known climatic sequences.

Finally, the undated dry period in the Late Pleistocene when the Sahara advanced 300 miles southward may perhaps be correlated with the stage postulated in the Striated Group when dry conditions prevailed on the ridge of higher country between the Cameroons and Uganda on which proto-*streptophorus* may eventually have been isolated.

All the other climatic changes I have postulated in Africa are relatively small and the occurrence of similar changes is unquestionable, though not necessarily in correct sequence. However, some of the dating for these in West Africa is interesting for the most recent humid period in the north-west (5,000–2,000 years ago) may be the time at which *F. bicalcaratus* spread into Morocco up the north-west coast, and if so the Morocco population, which shows only slight divergence, may have been isolated for only 2,000 years. The lack of divergence between the populations of *F. ahantensis* on either side of the present gap in the Upper Guinea forest also gives support to Moreau's evidence that the gap was once further east "probably as late as the Late Pleistocene".

In the Spotted Group of Asia, as in the African groups, it was postulated that the members developed to specific status after the last glaciation. While it is easier here to argue that the same sequence of isolating and rejoining of species was likely to take place in any glaciation it seems unlikely that the simple pattern which remains now could be the product of more than one such sequence.

Finally, lest any of the foregoing should sound dogmatic, it is necessary to end on the same note of caution that was sounded in the introduction. I am fully aware that all the conclusions are based on circumstantial evidence drawn from my interpretations of the picture as we see it today, which are necessarily fallible since so much of the picture is missing. That it has proved possible to construe the known facts into a logical and coherent story gives some verisimilitude to it and so does the evidence that many of the postulated vegetational changes have actually taken place. However, the story remains hypothetical, but further studies of this nature and researches in other branches of science will corroborate or disprove others of the possibilities suggested so that eventually a picture may emerge that approximates to reality.

SUMMARY

1. It is found that the genus *Francolinus* (including *Pternistis*) is comprised of eight groups, the members of which are largely allopatric, and four independent species.

2. Some of the difficulties are discussed of defining the relationship between the members of the groups.

3. The value of different characters as a guide to relationship is illustrated by comparison between the groups.

4. Each group is studied in turn and the characters and ranges of its component members defined. In doing this it was found necessary to review the systematics of the Redwing and Greywing Francolins of the species *africanus* (olim. *afer*), *levaillantoides* (olim. *gariiepensis*) and *shelleyi*.

5. An attempt is made to postulate the sequence of evolutionary stages through which each group has developed, and the climatic and vegetational changes which have accompanied each stage.

6. The four independent species are discussed.

7. Comparison between groups suggests that slight ecological divergence may be an especially effective barrier to interbreeding.

8. It is concluded that most members of groups reflect in their characters, relationship, and present ranges, the climatic changes that took place in the Late Pleistocene, subsequent to the last glaciation, or, in Africa, the last extensive spread of montane forest. Consequently it is suggested that the number of species of this status is liable to fluctuate considerably in glacial and inter-glacial periods, though the number of groups and independent species may remain more or less constant.

9. These conclusions are supported to some extent by evidence provided by R. E. Moreau of climatic changes that have taken place in the Late Pleistocene (Appendix 1), but more evidence is needed from all branches of science to evaluate them fairly.

APPENDIX 1

Summary of some conclusions reached by R. E. Moreau on the climatic fluctuations in Africa as set out in his paper "Vicissitudes of the African Biota in the Late Pleistocene" (in press : to be published in Proceedings Zoological Society, London).

Africa generally (in conformity with world temperatures)

Colder than the present (with associated reduced humidity) in varying degrees for at least 50,000 years prior to 18,000 years ago. In the last extreme phase, extending from about 24,000–18,000 years ago the cooling amounted to about 5°C. Around 7,000–5,000 years ago probably 2°C. warmer, and for some centuries prior to 150 years ago 1–2°C. cooler, than the present.

Mediterranean Africa and Northern Sahara

A major pluvial period affected at least the western half of the area in the late Middle Pleistocene, prior to perhaps 100,000 years ago. Palaearctic plants and land-

Footnote : Mr. Moreau has very kindly allowed me to include this summary to illustrate my paper but it must be appreciated that most of the conclusions quoted have been qualified in the full text, where reference is given for the authority on which they are based. This summary must not therefore be used as a base for further premises without consulting the full paper. It must be emphasized that the time-correlations of the events referred to in different parts of Africa remain to be worked out.

molluscs advanced some 400 miles southward and persisted in Ahaggar until the Neolithic, some 6,000 years ago.

Between 5,000 and 2,000 years ago it was more humid (at least in the north-west) than at present.

Southern edge of Sahara and sub-Saharan West Africa

The southern edge of the desert has fluctuated in the course of the Late Pleistocene (i.e. about the last 100,000 years) between about 300 miles south and 300 miles north of the present position and these changes probably extended across to the White Nile. Since the Neolithic, i.e. in about the last 5,000 years, a belt of country some 300 miles in width has reverted to desert.

These fluctuations affected the vegetation of coastal West Africa, especially the Upper Guinea forest, and when the desert came south of its present location the area of forest was greatly reduced and further dissected.

At some stage in the Late Pleistocene, not yet dated, Lake Chad increased to an area 600 miles long, extending nearly to Tibesti. This implies a contemporary northward extension (or movement) of the equatorial rain-belt by some 300 miles.

Prior to its capture by the Lower Niger, some 10,000 years ago, the Upper Niger expended itself in large lakes northwest of Timbuktu, in what is now extreme desert.

Congo basin and Angola

Late in mid-Pleistocene very dry, with aeolian re-distribution of Kalahari sand. Congo forest reduced to a strip towards the coast, another along the eastern rim of the basin and perhaps a third along the northern edge. Throughout Late Pleistocene, humid except in Katanga and Eastern Angola. Here arid in the latter part of the Late Pleistocene down to about 10,000 years ago.

East Africa

The "Gamblian" pluvial, with fluctuations in intensity was contemporary with the Last Glaciation and extended down to about 18,000 years ago, and there have been subsequently at least two short periods more humid than the present. Owing to the broken topography the vegetational effects would have been, in the main, local advances and retractions of vegetation types. In Somaliland the fluctuations were minor and the country always to some degree dry. (Note: There is evidence that at some period in the Early Pleistocene lowland forest extended at least to Oldowai in northern Tanganyika. Also at some period in the Late Pleistocene a corridor of acacia probably extended through Tanganyika to Northern Rhodesia).

Rhodesia and southern Africa

During the Late Pleistocene the rainfall fluctuated between about half and one and a half times the present in the Rhodesias and the Transvaal. Kalahari sand was blowing east as far as the Victoria Falls some 12,000–9,000 years ago. The Orange Free State was drier than the present some 40,000 years ago. South West Africa was never better than semi-arid,

APPENDIX 2

Taxonomic notes and synonymy

SPOTTED GROUP

F. francolinus

Five clinal races have been recognised and further sub-division does not seem useful. Therefore *caucasicus* and *sarudyni* are placed in the synonymy of *francolinus*; *festinus* Koelz, 1955 and *bogdanovi* in the synonymy of *henrici*; *parkeri* Van Tyne & Koelz, 1955 in the synonymy of *asiae*. Also *billypaynei* Meinertzhagen, 1933, which is a name given to an exceptionally dark micro-population from the Lake of Antioch, is included in *francolinus*.

F. pintadeanus

The characters on which *wellsi* was based do not seem constant and it is accordingly regarded as a synonym of *pintadeanus*.

I accept Delacour's opinion (1951: 10) that *F. boineti* Bourret, 1944 is an aberrant specimen of *F. pintadeanus*.

BARE-THROATED GROUP

F. leucoscepus

The amount of variation exhibited by the whole species is so slight that numerous sub-divisions are not practical. Accordingly *holtemulleri*, *muhammedbenabdullah*, *keniensis*,* *kiliensis*, *tokora*, *oldowai* Van Someren, 1939, are placed in the synonymy of *infuscatus*.

F. swainsonii

Since *Pternistis* has been submerged in *Francolinus*, *P. s. chobiensis* Roberts, 1932, is pre-occupied and *F. s. lundazi* used instead (see Benson & White, 1957: 138).

A record of the occurrence of *F. swainsonii* at Karonga, at the north end of Lake Nyasa (Long, 1961: 25) was based on a misidentification, the specimens being *F. afer* (Benson, *in litt.*).

F. afer

In the block of vermiculated subspecies there is much individual but little geographical variation. Accordingly *punctulata* and *nyanzae* are placed in the synonymy of *cranchii*.

In the black-and-white birds of Angola and South West Africa variation between the northern and southern birds is too slight to warrant recognition, so *palliditectus* White, 1958 (nom. nov. for *cuneneensis* Roberts) is placed in the synonymy of *afer*. In South Africa an intermediate population between *castaneiventer* and *notatus* was named *krebsi*, which I place in the synonymy of *castaneiventer*. In eastern Africa the name *humboldtii* was given to a bird from Tete on the Zambezi, a locality lying in the centre of the zone of hybrids between the black-faced *melanogaster* and the white-faced *swynnertoni*: it is here restricted to the unstable population.

If names are required for the hybrids between the vermiculated and black-and-white subspecies it is convenient in Angola to refer those populations which are closest to *cranchii* to *manueli* White, 1945 (synonyms *camabatelae* Meise, 1958, and *mackenziei* White, 1945), and those which are closest to *afer* to *benguellensis* (synonyms *angolensis* Bocage, *angolensis* Roberts, and *chio* Meise, 1958—see Traylor 1960a: 143–146). Similarly in Tanganyika, Nyasaland and the Luangwa valley those populations closest to *intercedens* may be known as *bohmi* (synonym *tornowi* Meise, 1933), and those closest to *melanogaster* may be known as *itigi* (synonym *aylwinae* White, 1947).

With the merging of *Pternistis* in *Francolinus* *F. coqui angolensis* Rothschild, 1902, is antedated by *Pternistes afer* var. *angolensis* Bocage, 1893, and by the laws of homonymy should be renamed. However Bocage's name *angolensis* was given in error to the same bird which he had named *benguellensis* at the head of his article, and the name was forgotten until listed in the synonymy of *Pternistis afer benguellensis* by Bowen (1930: 157). It thus has remained unused as a senior synonym in the primary zoological literature for more than fifty years and must be considered a forgotten name (nomen oblitum). (Int. Code of Zool. Nomen. 1961. Article

* Also pre-occupied by *F. squamatus keniensis* Mearns, 1910.

23b.) Application is being made to the International Commission for it to be placed on the Official Index of Rejected Names.

MONTANE GROUP

F. castaneicollis

It is probable that most of the micro-populations in isolated patches of evergreen forest are slightly distinct, but it is not practical to recognise by name all those that show minor differences: accordingly *vottegi* and *gofanus* are placed in the synonymy of *castaneicollis*, and *parizii* Toschi, 1958, in the synonymy of *kaffanus*.

F. jacksoni

It has not been established that variation in the amount of white in the underparts is geographical or associated with altitude. Therefore *gurae* is placed in the synonymy of *jacksoni*.

F. nobilis

F. camerunensis ruandae Van Saceghem, 1942, is placed in the synonymy of *F. n. nobilis*. It is also pre-occupied by *F. coqui ruandae* Jackson, 1938.

F. swierstrai

F. cruzi Themido, 1935, is placed in the synonymy of *F. swierstrai*.

SCALY GROUP

F. squamatus

Although there is considerable individual variation no significant geographical variation is recognised from the greater part of the range. Accordingly *tetraoninus*, *zappeyi* and *dowashanus* are placed in the synonymy of *schuetti* and *whitei* Schouteden 1954 (*nom. nov.* for *confusa* Schouteden 1954) in the synonymy of *squamatus*.

It is not thought practical to recognise by name any micro-populations isolated on the mountains of the Kenya/Tanganyika border, since the main trend of variation is clinal. Therefore, *kapitensis*, *keniensis* and *chyuluensis* Van Someren, 1939 are placed in the synonymy of *maranensis*.

VERMICULATED GROUP

F. bicalcaratus

It has been shown that birds become darker and more heavily patterned towards the south-east of the range, but the differences exhibited in this cline do not seem great enough to warrant separating the birds of the extreme south-east from those of the southern (British) Cameroons. Accordingly *molunduensis* Grote, 1949, is synonymised with *ogilviegranti*.

F. icterorhynchus

The clinal variation does not warrant more than a division into two subspecies. Accordingly *griseus* is placed in the synonymy of *icterorhynchus* and *emini* and *ugandensis* in the synonymy of *dybowskii*. Birds showing a few chestnut feathers on the flanks, the character on which *ugandensis* was founded, occur sporadically in south-eastern Uganda and must be considered aberrant specimens perhaps indicating past hybridisation with *clappertoni*.

F. clappertoni

F. tschadensis is placed in the synonymy of *F. c. clappertoni* (see text).

The clinal variation shown in southern populations does not warrant extensive splitting; accordingly *cavei* Macdonald, 1940, and *testis* are placed respectively in the synonymy of *gedgii* and *sharpii*.

F. hildebrandti

Numerous subdivisions are not practical; accordingly *helleri* is placed in the synonymy of *hildebrandti*, and *grotei* and *lindi* in that of *johnstoni*.

F. natalensis

The name *thamnobium* Clancey, 1953, was proposed to distinguish paler birds inhabiting drier areas from those of wetter habitats in Natal and the Zoutspansberg (*natalensis*), but since this

gives *natalensis* a discontinuous range it is not practical to recognise the differences by name.

F. hartlaubi

ovambensis is considered a synonym of *bradfieldi*.

F. adspersus

kalahari is considered a synonym of *adspersus*.

STRIATED GROUP

F. sephaena

The name *somaliensis* Grant & Praed, 1934, was given to streaked birds from Somaliland and was based on the misapprehension that the type of *spilogaster* was an unstreaked bird (Rand, 1950: 384). As noted in the text I believe *spilogaster* must be used for the hybrid populations from Somaliland to southern Kenya. However, if it is established that there still exists an unmixed population of streaked birds on the coastal plains which is distinct from the southern *rovuma* then the name *somaliensis* is available. Such a population can be assumed to have existed once since it must be regarded as one of the parents of the hybrid *spilogaster* but it may have been integrated into the hybrid population.

Local variations in size, colour and pattern throughout the species do not seem great enough to distinguish by name. Accordingly *zuluensis* is placed in the synonymy of *sephaena*: *thompsoni*, *chobiensis*, *mababiensis* in the synonymy of *zambesiae*: *schoanus*, *ochrogaster* Hartlaub, 1882, *delutescens*, and *jubaensis* in the synonymy of *grantii*: Peters (1934: 73) shows that *rovuma* antedates *kirkii*.

RED-WINGED GROUP

F. psilolaemus

On the author's own showing *fricki* is regarded as a synonym of *F. p. ellenbecki* (Friedmann, 1930: 113).

F. shelleyi

There is not sufficient variation between the populations of South Africa and Tanganyika to justify the recognition of *trothae* which is regarded as a synonym of *shelleyi*, as is *sequestris* Clancey, 1960.

F. africanus

Praed & Grant have been among the few modern authors who have correctly regarded *Perdix afra* Latham, 1790, as the senior name of the South African Greywing, known by others as *F. africanus* Stephens, 1890. However, since the submersion of *Pternistis* in *Francolinus*, *Perdix afra* Latham is pre-occupied by *Tetrao afer* Muller 1776, the senior name for the bare-throated francolin formerly known as *Pternistis afer*. The Greywing must therefore now be known as *F. africanus*.

Within the range of the species there is slight local variation but it is not great enough for me to recognise any subspecies: *proximus* Clancey, 1957, is therefore placed in the synonymy.

F. levaillantoides

Roberts (1936: 321) shows that *F. levaillantoides* is the original name for this species and *garipeensis* is a synonym.

In this species the haphazard distribution of rufous and grey micro-populations in the southern districts of the Sudan and Abyssinia and in Angola and South West Africa makes it difficult to know how many subspecies can usefully be recognised. I believe it is impractical to attempt to differentiate between these variations if no other differences are shown, and, furthermore, names should not be used for intermediate populations. Accordingly I recognise in the south—

(a) *F. l. levaillantoides*. All districts east and south of the Kalahari, intergrading with *kalaharica* on the fringes of the Kalahari. Richly coloured (even in the greyest specimens) and heavily patterned. Synonyms, *ludwigi* and *garipeensis*.

(b) *F. l. kalaharica* (Roberts) 1932. The Kalahari. Pale and grey, birds from central

districts almost unmarked on the abdomens; birds from the fringes rather darker with more markings on the abdomen. Synonym, *langi* Roberts, 1932. (Although *langi* has line priority over *kalaharica* I use *kalaharica*, as I am entitled to do as first revisor, since the name was given to a very pale, grey bird from the Damara Pan near the centre of the Kalahari, and thus represents the extreme of variation, while *langi* was given to a rather darker bird from Nkate near the eastern border.)

- (c) *F. l. pallidior*. South West Africa. Either rufous or grey but the rufous birds paler in tone than *levaillantoides*, and the grey birds darker and more heavily marked than *kalaharica*. As known at present the population of the Windhuk area is more rufous, and that of the Tsumeb area greyer (approaching *kalaharica*). Synonym *wattii* Macdonald, 1953. (See Macdonald, 1953, for detailed discussion.)
- (d) *F. l. jugularis*. Southern Angola to the Cunene. Differs from all other subspecies in having a broad black-and-white gorget: typical birds from the Benguela area are small and grey but those from the Cunene are larger and more rufous showing an approach to some of the populations of *pallidior*. Synonyms, *cunenensis* Roberts, 1932, *stresemanni* Hoesch & Niethammer, 1940.

In the north—

- (e) *F. l. archeri*. Extreme southern Sudan to the Golis range of western (British) Somaliland. Similar to *F. l. pallidior* in having both rufous and grey populations but in both the abdomens are paler and commonly marked with fine lines. Synonyms *friedmanni* Grant & Praed, 1934, *stantoni* Cave, 1940.
- (f) *F. l. lorti*. Mountains of eastern (British) Somaliland. Very grey, with a very pale abdomen fairly heavily marked with fine lines.
- (g) *F. l. gutturalis*. Northern Abyssinia and Eritrea. Quite distinct (see text). Synonym *eritrea* Zedlitz.

F. levaillantii

A number of names have been given to the birds of the northern and western populations which have no black-and-white stripe down the ochre collar on the hind neck. However, while the few specimens available indicate that there is a tendency for Angola birds to be paler, the difference is trivial and the series otherwise is remarkably uniform. Accordingly *mulemae*, *adolfriederici*, *benguellensis* Neumann, 1908, *clayi* White, 1944, and *momboloensis* White, 1952 (nom. nov. for *benguellensis*) are placed in the synonymy of *kikuyuensis*.

THE RED-TAILED GROUP

F. coqui

In the populations of central and south-eastern African there is considerable individual and local variation in size and colour so that consistent geographical variation is hard to determine. I do not believe it is practical to distinguish from nominate *coqui* the small coastal birds of Kenya since equally small birds are found in Natal, or to distinguish the populations of Natal, Zululand and southern Mozambique, which on the whole are less rufous, for individuals can be matched with others elsewhere. The names *stuhlmanni* and *campbelli* are therefore placed in the synonymy of *coqui*. I regard *lynesi* Sclater, 1932, also as a synonym of *coqui* since the type is intermediate between *coqui* and *kasaicus* but comes from an area in which the majority of specimens are closest to *coqui*.

For the Uganda race the original spelling "*ruahdae*" has been used since, while the author may have intended the name to be "*ruandae*", there is no clear evidence of this intention in the original publication. (Int. Code of Zool. Nomen. 1961, Article 32a (ii).) *F. coqui ruandae* Jackson, 1938, is accordingly a junior objective synonym. (Article 33a (ii).)

F. albogularis

Serle (1957: 388) shows that *gambagae* must be considered a synonym of *buckleyi*.

The isolated populations of Marungu and Upemba in the south-eastern Congo, the Balovale district of Northern Rhodesia, and of eastern Angola seem to show an increase from east to west in the amount of patterning in the females, and the Angola birds seem also to be darker,

less rufous, than others (Hall, 1960a: 409). Too few specimens are available at present on which to judge the extent of variation, and until there are more, especially of topotypical *meinertzhageni* from Rhodesia, it seems best to use *meinertzhageni* for Rhodesian and Angola birds and *dewittei* for the Congo birds, though I believe that the Rhodesian birds may prove to be closer to those from the Congo than to those from Angola.

F. schlegelii

Traylor (1960: 86) has shown that *confusus* Neumann, 1933, should be considered a synonym of *schlegelii*.

SPECIES NOT INCLUDED IN ANY GROUP

F. pondicerianus

It has been shown that variation in this species is slight and largely clinal and ecological. It is not practical to recognise more than one intermediate subspecies. Accordingly *paganus* Koelz, 1954, *titar* Koelz, 1954, *prepositus* Koelz, 1954, are all placed in the synonymy of *interpositus*.

SPOTTED GROUP—MAP 1

The shaded areas represent the overall ranges of the species. The thick red line indicates divisions between species. The thin red line indicates divisions between subspecies, the zig-zag line denoting intergradation. The red crosses indicate localities from which hybrid specimens have been obtained.



F. francolinus

1. *francolinus*
2. *arabistanicus*
3. *henrici*
4. *asiae*
5. *melanotus*



F. pictus

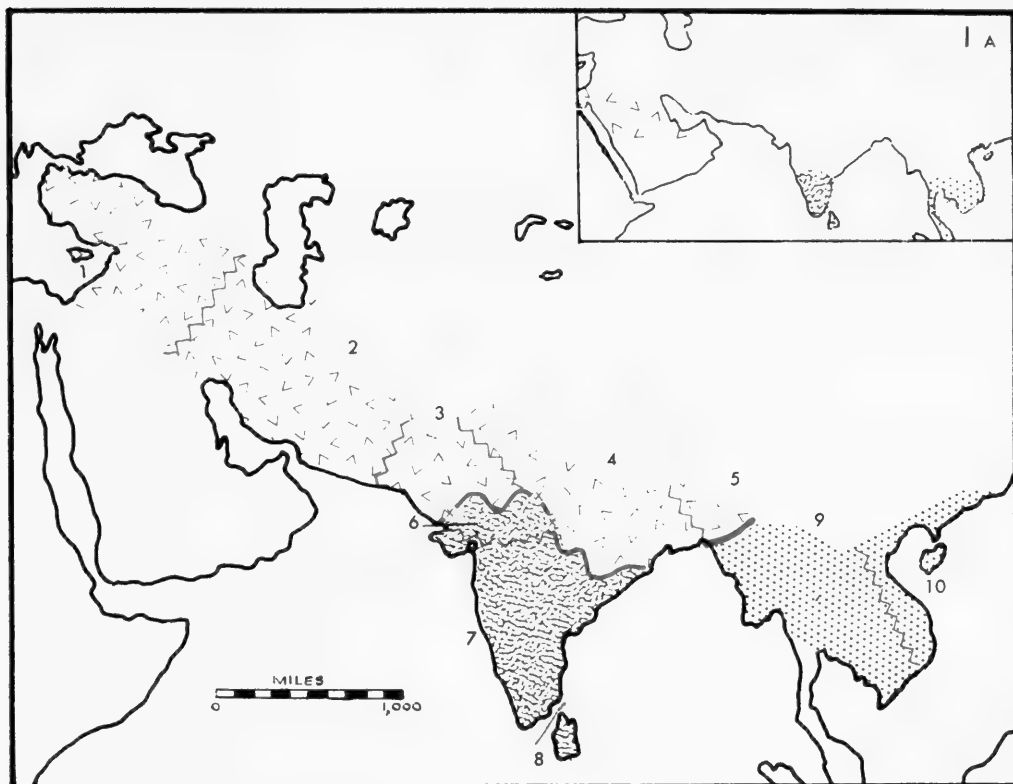
6. *pallidus*
7. *pictus*
8. *watsoni*



F. pintadeanus

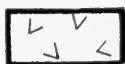
9. *phayrei*
10. *pintadeanus*

MAP. 1A. Hypothetical distribution of the ancestral stock of the three species during a glaciation (Stage 2).

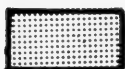


BARE-THROATED GROUP—MAP 2

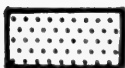
Overall ranges are shown rather than precise collecting localities. Thick red lines denote specific boundaries. Thin red lines denote subspecific boundaries, plain lines being boundaries between non-intergrading subspecies, zig-zag lines boundaries between intergrading subspecies, toothed lines boundaries of hybrid zones. The red "X" marks the area of hybrids *swainsonii* × *afer*. Numbers have been given only to species and subspecies which are important to the discussion on speciation, but the ranges of other subspecies are indicated.



1. *F. leucoscepus* (*leucoscepus*, *infuscatus*)



2. *F. rufopictus*



3. *F. swainsonii* (*swainsonii*, *lundazi*, *damarensis*, *gilli*)



F. afer. Black-and-white, "afer-type" subspecies

4. *castaneiventer* & *notatus*

5. *lehmanni*

6. *swynnertoni*

6 × 7. hybrids (*humboldtii*)

7. *melanogaster* & *loangwae*

8. *leucoparaeus*

9. *afer*



Vermiculated, "cranchii-type" subspecies

10. *cranchii* & *intercedens*

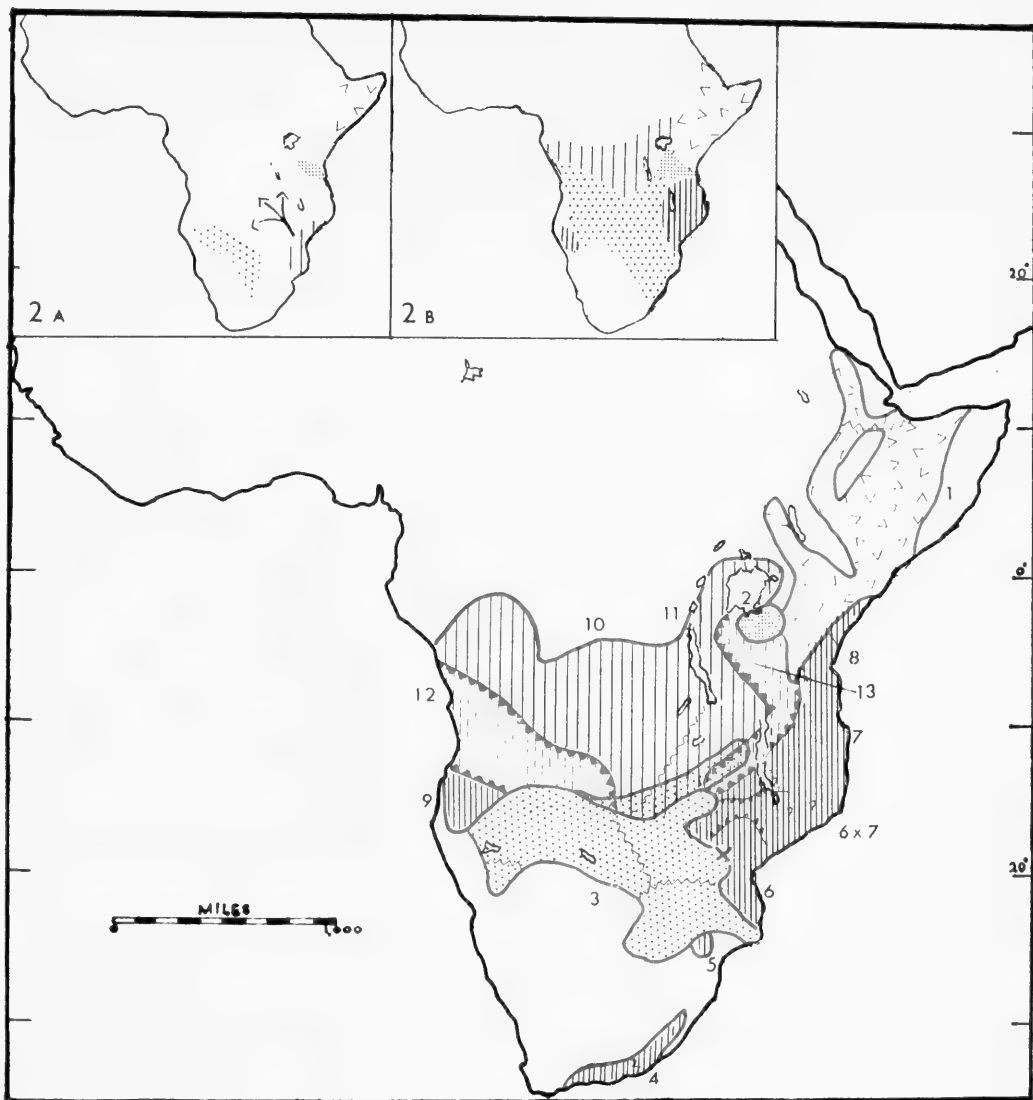
11. *harterti*



Hybrids between "afer-type" and "cranchii-type" subspecies.

MAP 2A. Hypothetical distribution of the ancestral stock of the four species during a spread of forest (Stage 4).

MAP 2B. Hypothetical distribution of the ancestral stock of the four species and two main blocks of *afer* subspecies during a later dry period (Stage 6).

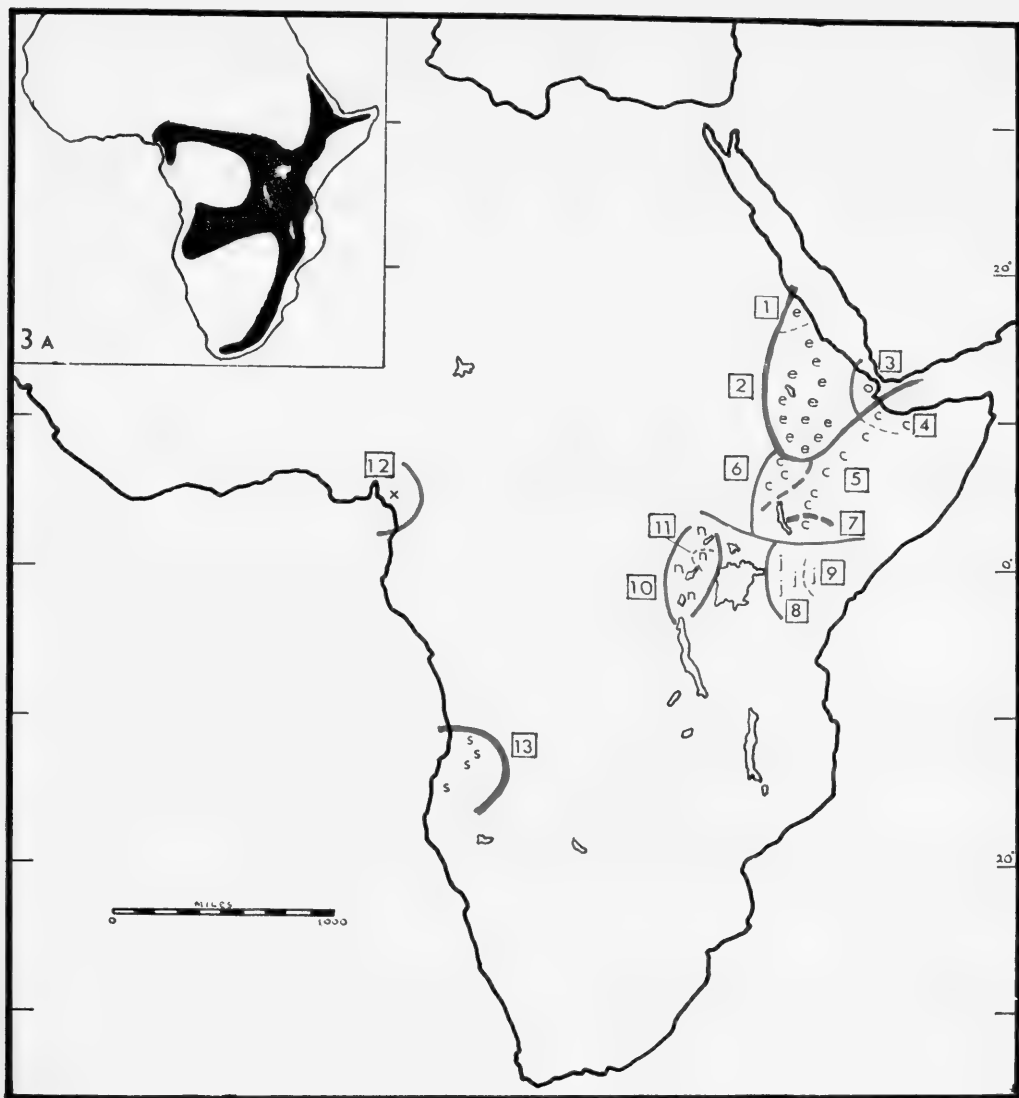


MONTANE GROUP—MAP 3

The letters indicate precise localities from which specimens have been collected. Plain red lines denote divisions between isolates which are regarded as species, and broken lines between those regarded as subspecies. The thickness of the lines is relative to the degree of divergence between neighbouring forms.

e	F. erckelii	1. <i>pentoni</i> 2. <i>erckelii</i>
o	F. ochropectus	3. <i>ochropectus</i>
c	F. castaneicollis	4. <i>ogoensis</i> 5. <i>castaneicollis</i> 6. <i>kaffanus</i> 7. <i>atrifrons</i>
j	F. jacksoni	8. <i>jacksoni</i> 9. <i>pollenorum</i>
n	F. nobilis	10. <i>nobilis</i> 11. <i>chapini</i>
x	F. camerunensis	12. <i>camerunensis</i>
s	F. swierstrai	13. <i>swierstrai</i>

MAP 3A. Hypothetical distribution of montane forest (shaded black) in a cold, wet era (Stage 1).



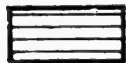
SCALY GROUP—MAP 4

A continuous distribution has been shown for members of the Scaly Group through the Upper and Lower Guinea forests, along the escarpment of Angola, and in the wetter areas of Uganda and Kenya, for within these areas the birds may be expected in suitable clearings or cultivations. Outside this range only general localities from which specimens have been collected have been shaded. Broad red lines indicate divisions between species: thinner red lines denote divisions between subspecies, those that intergrade being indicated by a zig-zag line. Thicknesses of the subspecific lines are relative to the divergence shown by neighbouring forms.



F. *ahantensis*

1. *hopkinsoni*
2. *ahantensis*



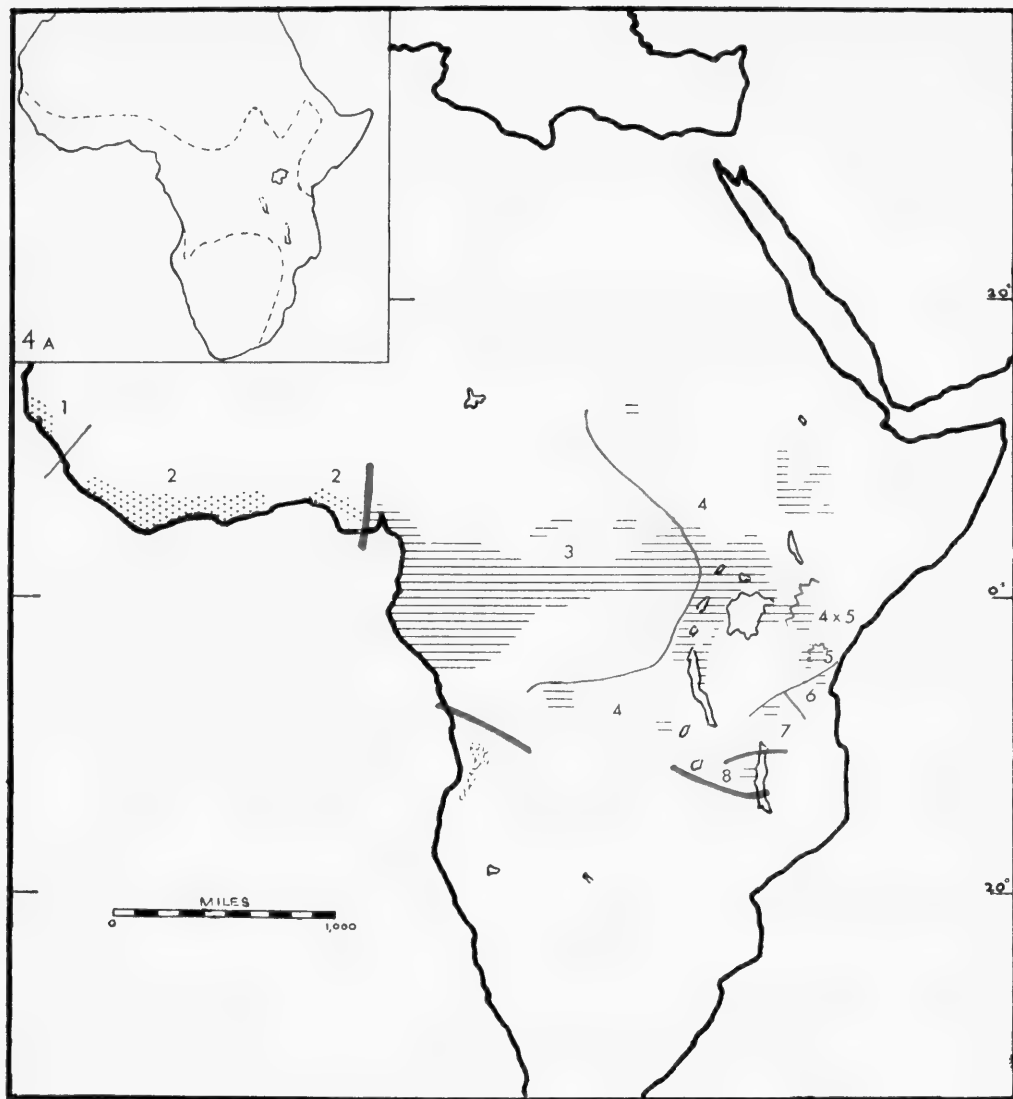
F. *squamatus*

3. *squamatus*
4. *schuetti*
5. *maranensis*
6. *usambarae*
7. *uzungwensis*
8. *doni*



F. *griseostriatus*

MAP 4A. Hypothetical map showing extent of lowland forest in a warm, wet era (Stage 5). Limits of forest shown by broken line.



VERMICULATED GROUP—MAP 5

The distribution of many members of this group is known to be discontinuous. Accordingly only general areas from which specimens have been collected are shaded, but the birds may be expected to occur in some of the intervening areas in which little collecting has been done. Thick red lines denote divisions between species: where there is evidence of hybridisation these lines are toothed. Thin red lines denote divisions between subspecies, those that intergrade being shown with a zig-zag line. The red "X" denotes a hybrid between *hildebrandti* and *natalensis*. The red "T" denotes the aberrant or hybrid specimen *F. tschadensis*. The red "U" denotes the area in which the aberrant "*ugandensis*"-type birds are found.



F. bicalcaratus

1. *ayesha*
2. *bicalcaratus*
3. *adamauae*
4. *ogilviegranti*
5. *thornei*



F. clappertoni

6. *clappertoni*
7. *gedgii*
8. *heuglini*
9. *sharpii*
10. *konigseggi*
11. *nigrosquamatus*



F. icterorhynchus

12. *dybowskii*
13. *icterorhynchus*



F. hildebrandti

14. *altumi*
15. *hildebrandti*
16. *johnstoni*



F. natalensis

17. *neavei*
18. *natalensis*



F. hartlaubi

(*hartlaubi*, *bradfieldi*, *crypticus*)



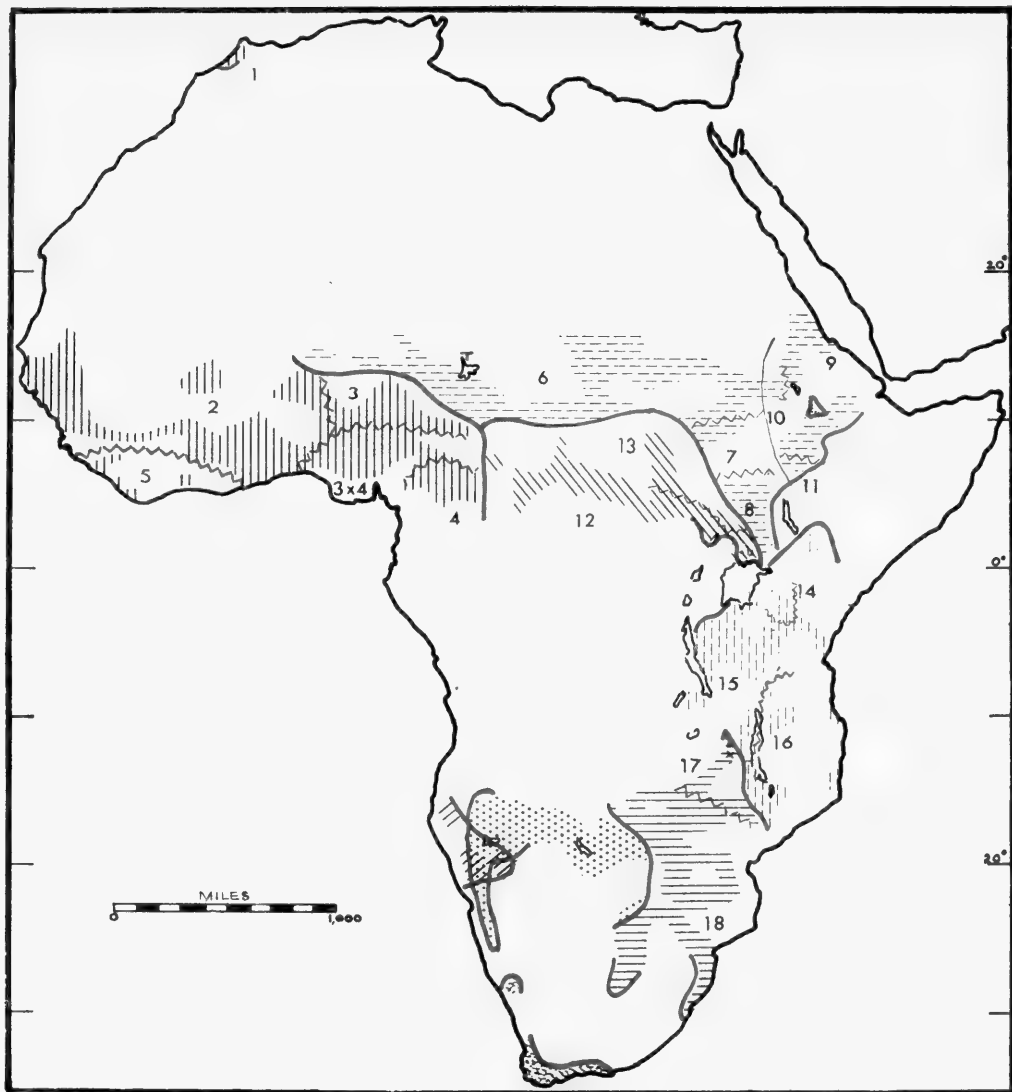
F. capensis



F. adpersus



F. harwoodi

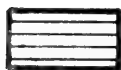


STRIATED GROUP—MAP 6

Only general areas from which birds have been collected are shaded. The broken thick red line indicates the outer limits of the range of *F. streptophorus*, and the unbroken thick red line the outer limits of the range of *F. sephaena*. Thin red lines indicate subspecific divisions, plain lines denoting divisions without intergrading, zig-zag lines denoting intergrading, and toothed lines denoting the boundary of a hybrid area.



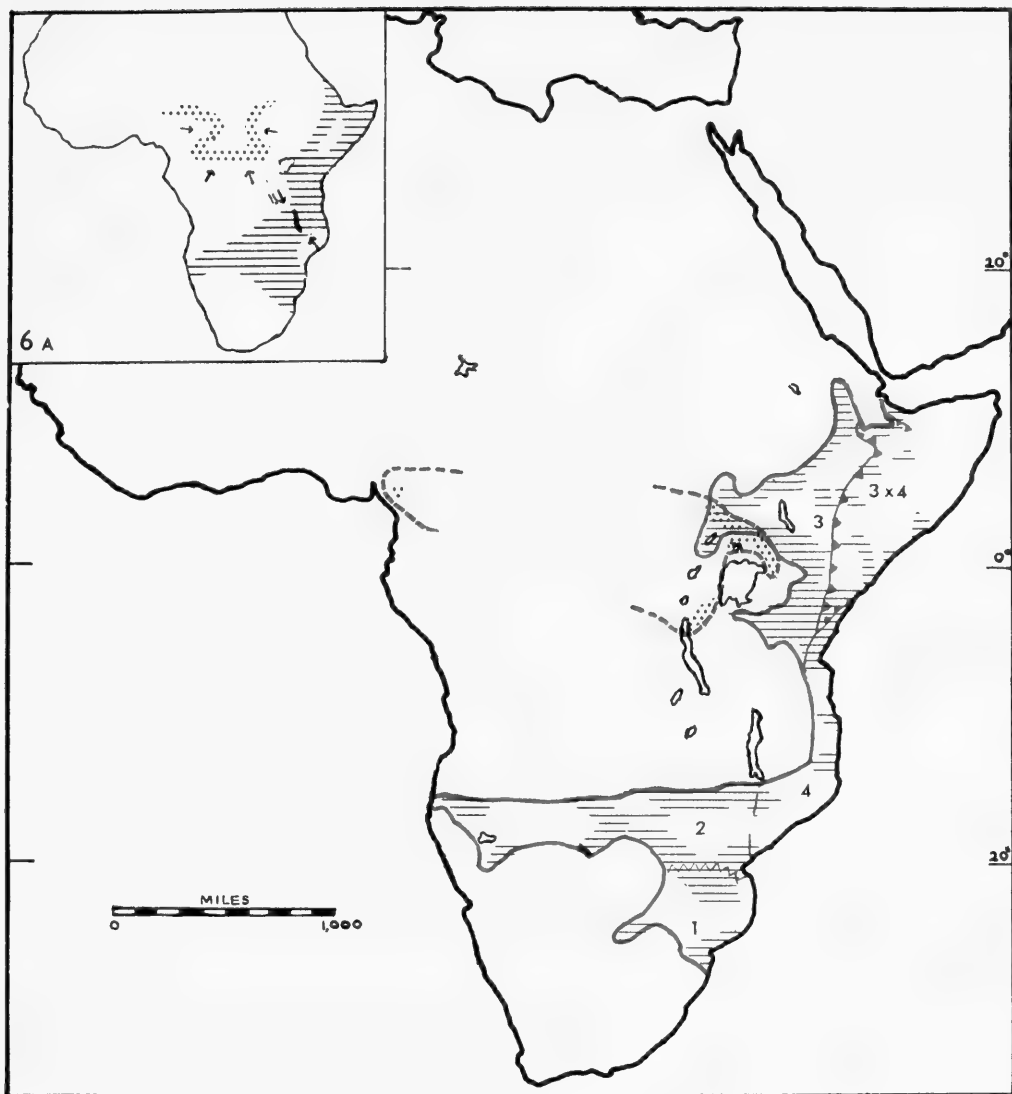
F. streptophorus



F. sephaena

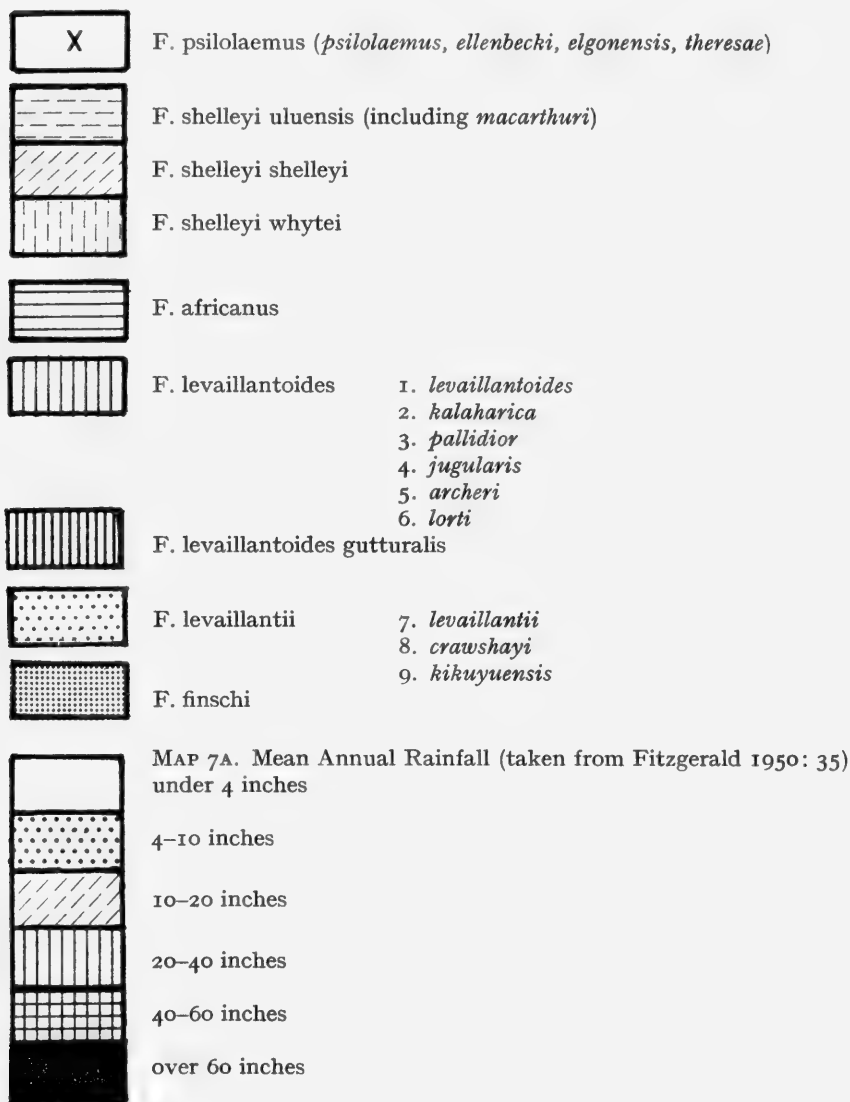
1. *sephaena*
2. *zambesiae*
3. *grantii*
- 3 × 4. *spilogaster*
4. *rovuma*

MAP 6A. Hypothetical distribution of the ancestral stock of the two species at the end of a dry era (Stage 4). Arrows indicate the line of advance of encroaching woodlands.

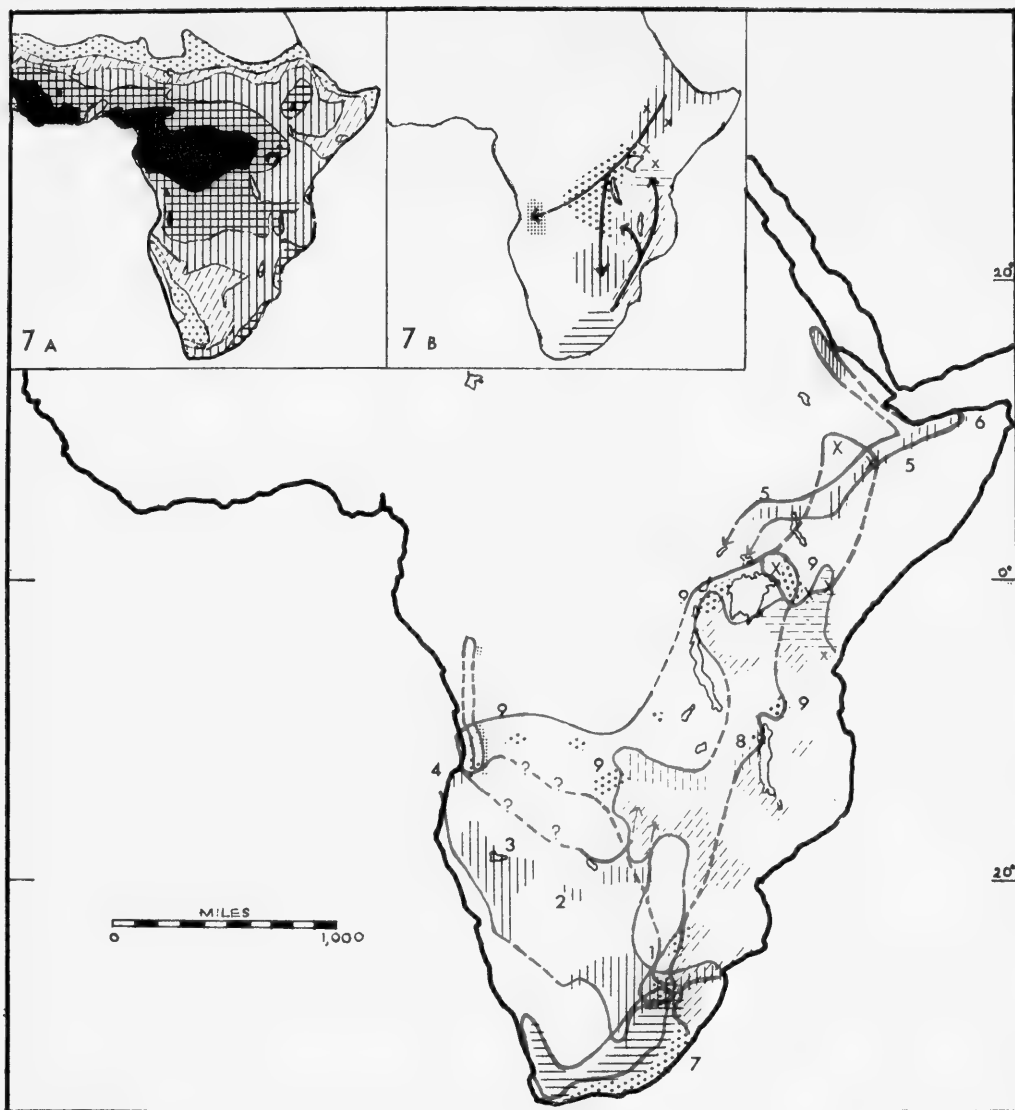


RED-WINGED GROUP—MAP 7

The distribution of all members of this group is discontinuous, accordingly only general areas from which birds have been collected are shaded. Thick red lines denote the extreme limits of the range of each species: these lines are broken where they link remotely isolated populations, except in *F. levaillantoides* where arrows indicate where the lines linking the northern and southern populations might fall. Lineal divisions between subspecies are not shown but different shading has been used for those subspecies which are strongly differentiated: others are numbered. The red cross indicates the Amani specimen which is intermediate between *F. s. shelleyi* and *F. s. uluensis*.



MAP 7B. Diagrammatic map showing hypothetical colonisation routes and centres of speciation (Stages 3–6).



RED-TAILED GROUP—MAP 8

The distribution of all members of this group is discontinuous and only general areas from which specimens have been collected are shaded. Thick red lines denote the extreme limits of the ranges of species, those linking remotely isolated populations being broken, except between the north-western and southern populations of *F. albogularis* where the link is indicated by arrows. Subspecific divisions are shown lineally only in the critical area of Kenya and Tanganyika. Here a toothed line surrounds a population which appears to be a result of hybridisation but which does not now intergrade with neighbouring subspecies: zig-zag lines indicate intergrading. Outside this critical area all subspecies, if not isolates, intergrade.



F. coqui

1. *coqui*
2. *vernayi*
3. *hieschianus*
4. *angolensis*
5. *kasaicus*
6. *ruahdae*
7. *hubbardi*
8. *thikae*
9. *maharao*
10. *spinetorum*



F. schlegelii

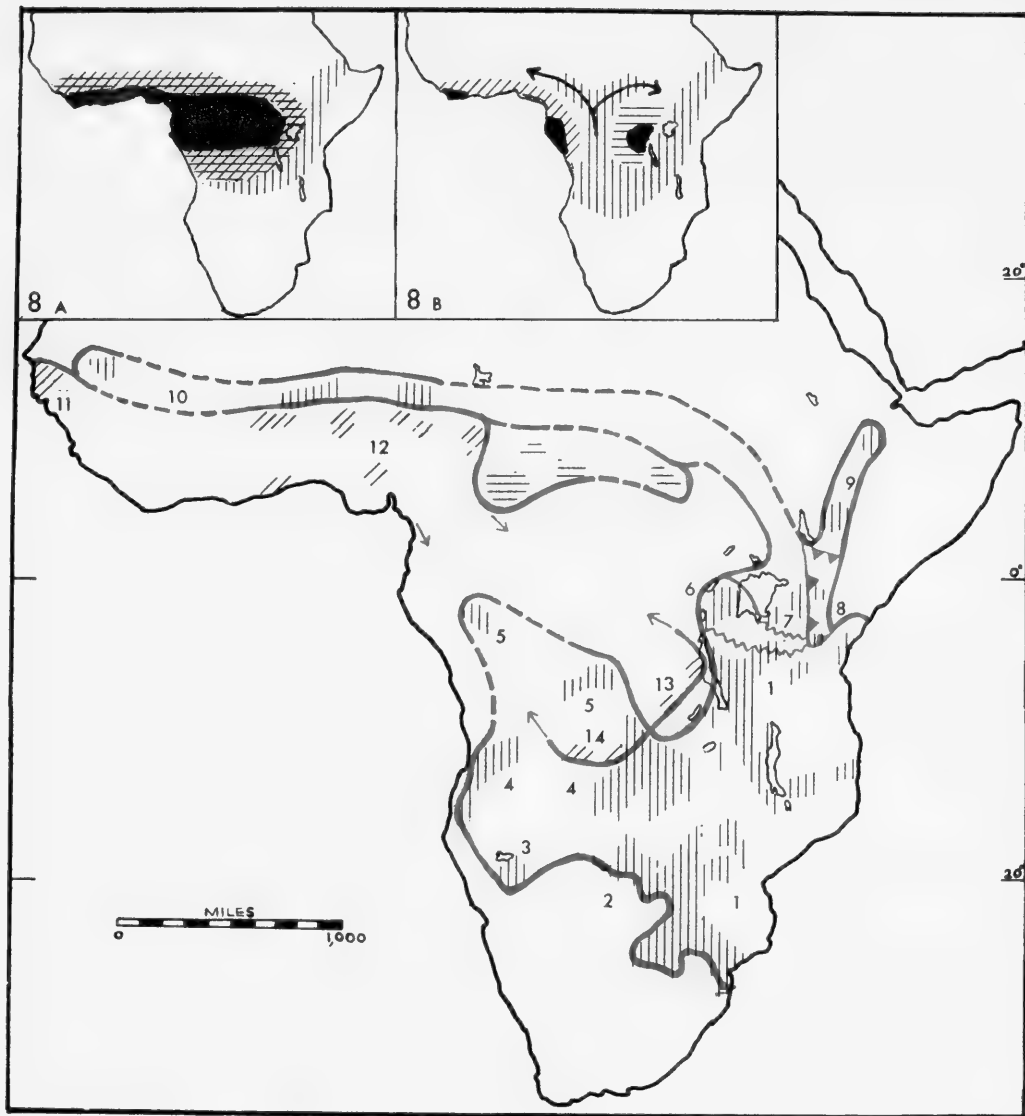


F. albogularis

11. *albogularis*
12. *buckleyi*
13. *dewittei*
14. *meinertzhageni*

MAP 8A. Hypothetical distribution of the ancestral stock of *F. coqui* and proto-*albogularis*/*schlegelii* (shown by mixed diagonal and horizontal shading) before the two latter species diverged (Stage 3). Distribution of lowland forest shown in black.

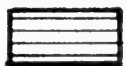
MAP 8B. Hypothetical distribution of the ancestral stock of the three species in a subsequent dry era (Stage 4).



SPECIES NOT INCLUDED IN ANY GROUP
MAP 9



F. nahani



F. lathami

1. *lathami*
2. *schubotzi*



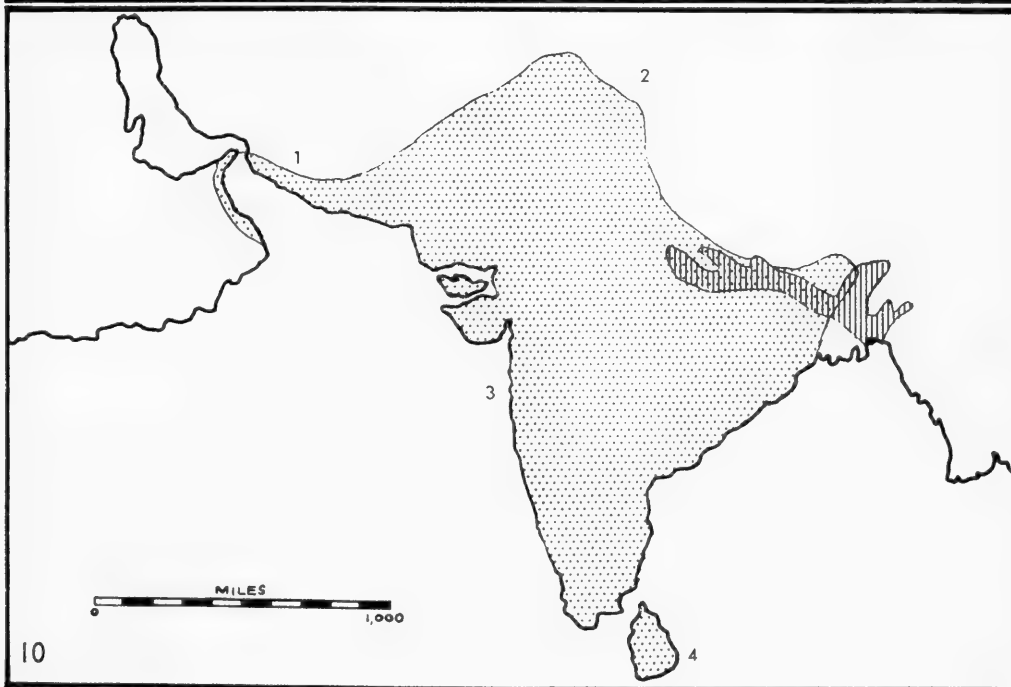
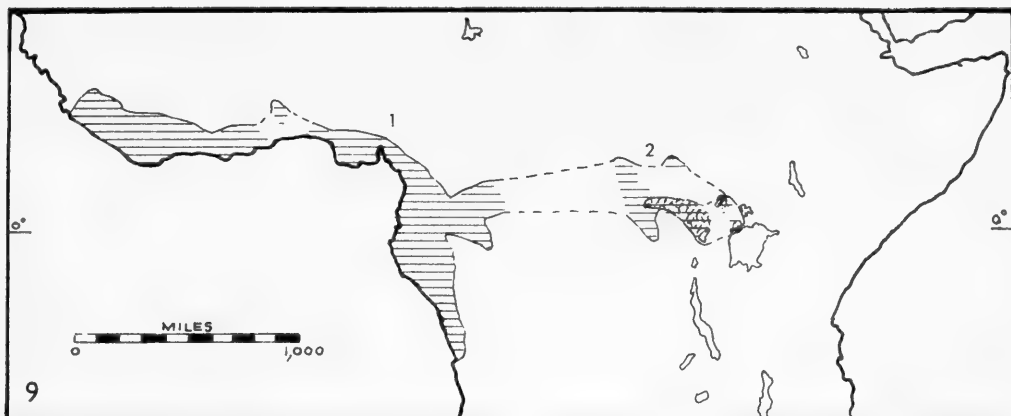
F. pondicerianus



F. gularis

MAP 10

1. *mecranensis*
2. *interpositus*
3. *pondicerianus*
4. *ceylonensis*



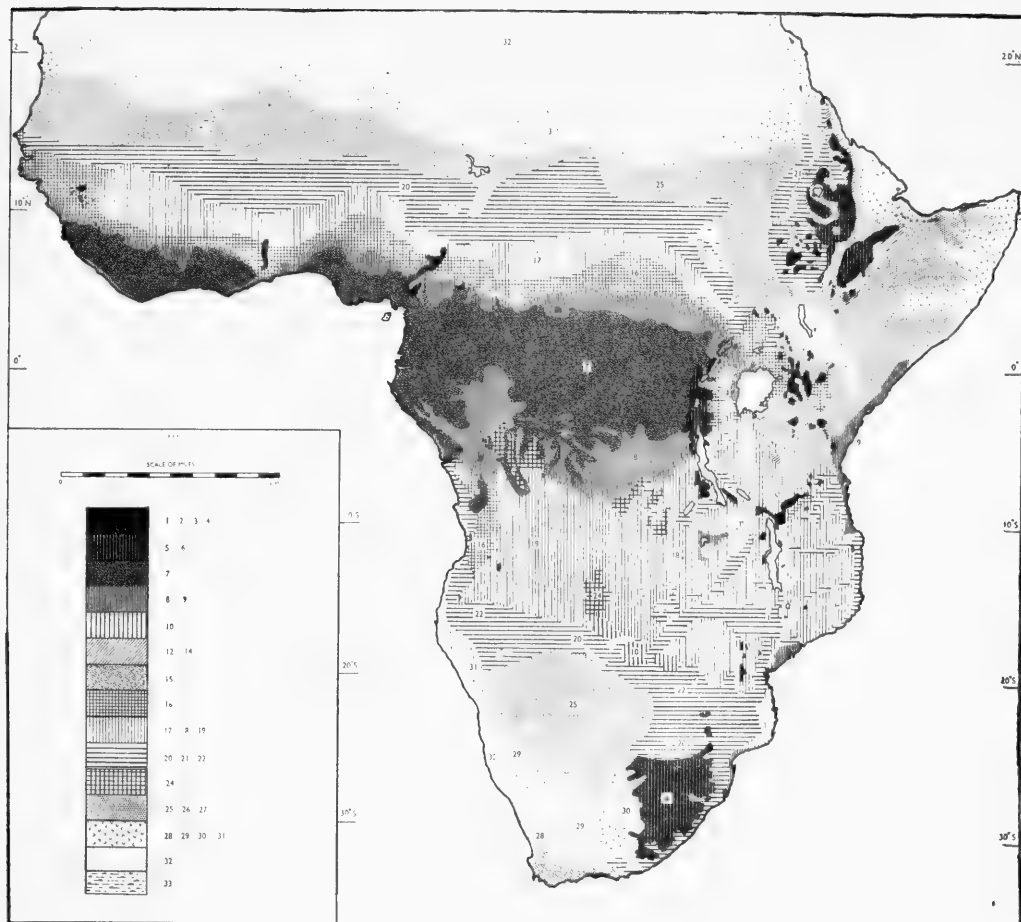
VEGETATION MAP OF AFRICA—MAP 11

Adapted from "Vegetation Map of Africa south of the Tropic of Cancer", Oxford University Press, 1959.

The numbering and terminology of the original map have been used as far as possible, excluding Madagascar. Explanatory notes indicating geographical areas are given in the key in cases where it is not possible to differentiate on the map between vegetation types.

KEY

- 1-4. EVERGREEN FORESTS & MONTANE COMMUNITIES.
 1. Montane Evergreen Forest.
 2. Temperate and Subtropical Evergreen Forest. *Knysna and other districts of the extreme south only.*
 3. Montane Communities—undifferentiated. These include evergreen forest (type 1), grassland (type 5) and woodland.
 4. Montane Communities—with afro-alpine communities. *High mountains of central and east Africa and Ethiopia only.*
(It has not been possible on this scale to distinguish between types 1, 3, and 4.)
- 5-6. MONTANE & HIGH ALTITUDE GRASSLAND.
 5. Montane Grassland above 6,000 ft. *North-eastern and central Africa.*
 6. Temperate and Subtropical Grassland. *Pure grassland above 3,500 ft. in South Africa.*
7. MOIST FOREST AT LOW AND MEDIUM ALTITUDES.
- 8-9. FOREST-SAVANNA MOSAIC.
 8. Moist forest surrounded by savanna of tall grasses. *Found in belts surrounding type 7.*
 9. Coastal Forest-Savanna Mosaic. *East coast only.*
10. DRY & DECIDUOUS FOREST—with abundant *Baikiaea plurijuga*. *Found only in parts of N. & S. Rhodesia, Bechuanaland and the Caprivi Strip, and sometimes regarded as woodland rather than forest.*
- 12 & 14. THICKETS.
 12. Itigi type. *Central Tanganyika only.*
 14. Ethiopian evergreen type. *Ethiopia only.*
15. CAPE MACCHIA.
16. RELATIVELY MOIST WOODLANDS. Types in which the genera *Isobertlinia*, *Brachystegia*, and *Julbernardia* are absent or rare.
- 17-19. WOODLANDS (interspersed with Savanna).
 17. With abundant *Isobertlinia doka* and *I. dalzielii*. *Northern areas.*
 18. With abundant *Brachystegia* and *Julbernardia*—"myombo". *Tanganyika to central Northern Rhodesia, Southern Rhodesia and Mozambique.*
 19. Similar to type 18 but with a number of distinctive species. Principally on Kalahari sand. *Angola to western N. Rhodesia.*
- 20-22. RELATIVELY DRY WOODLANDS & SAVANNAS.
 20. With frequent *Acacia* but other species as well, and savannas of tall grass with certain species of *Acacia*.
 21. Ethiopian types. A heterogeneous assemblage of low deciduous shrubs on stony ground. *Ethiopia only.*
 22. With abundant *Colospermum mopane*. *Southern Africa only.*
24. GRASS STEPPE ON KALAHARI SAND.



25. STEPPES.
 25. Wooded steppe with abundant *Acacia* and *Commiphora*.
 26. Grass steppe with thicket clumps. *Western Uganda only*.
 27. Grass steppe—Luanda type. *Coastal Angola only*.
 28–31. KAROO & SUBDESERT STEPPE.
 28. Karoo Succulent Steppe. *Western Cape Province only*.
 29. Karoo shrub and grass. *Cape Province and southern South West Africa*.
 30. Transitional and mixed Karoo. *East-central Cape Province*.
 31. Northern areas and northern South West Africa and southern Angola.
 32. DESERT.
 33. SWAMPS.

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INDEX TO SPECIFIC AND SUBSPECIFIC NAMES OF *FRANCOLINUS*

Specific and subspecific names of francolins are listed under the nomenclature used in this paper, those of species and subspecies here recognized appearing in roman type, others in italics.

No attention is paid to other generic names that have been given to francolins except in a few cases where the merging of these names in *Francolinus* has created homonyms.

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P. J. MILLER



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BY

P. J. MILLER

(Department of Zoology, The University, Glasgow, W.2)

Pp. 205-256 ; *Plate* ; 21 *Text-figures*



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TAXONOMY AND BIOLOGY OF THE GENUS *LEBETUS* (TELEOSTEI-GOBIOIDEA)

By P. J. MILLER

ABSTRACT

The marine gobioid genus *Lebetus* Winther 1877 is redefined and previous division into two species—*orca* Collett 1874 and *scorpioides* Collett 1874—shown to be based on sexual dimorphism in one species, by page priority *L. orca*. A redescription of the species is provided including details of sensory papillae and osteology. *L. orca* is eastern Atlantic boreal in distribution, occurring as a small predator on coarser grounds down to 375 m. Specialization of the male genitalia and sexual dimorphism are described and the breeding season provisionally regarded as from March to August. The skeleton of *Lebetus* is typically gobiid, and evidence is presented for a closer relationship to the genus *Buenia* Iljin as represented by *B. jeffreysii* (Günther) than to the Mediterranean *Odondebuena* De Buen and *Cabotichthys* Whitley with which *Lebetus* had been previously grouped.

INTRODUCTION

THE genus *Lebetus* was founded by Winther (1877) to contain two species of gobies dredged by G. O. Sars on the coast of Norway and described by Collett (1874) as *Gobius orca* and *G. scorpioides*. These species have subsequently been regarded as among the rarest of European Atlantic fishes and, until recent years, the numbers of demersal individuals known to science have been relatively few. In the last fifteen years, protracted dredging surveys off the Isle of Man (Jones, 1951; Hartnoll, 1961) have yielded many examples. Their small size and occurrence on rough grounds makes collecting difficult; in Manx waters, most specimens have been obtained by means of a scallop dredge lined with shrimp netting. Relative infrequency of capture is probably due to inadequacies of the fishing gear rather than to actual rarity, and occasional hauls providing up to five individuals suggest the presence of appreciable numbers in the area. Other long term faunistic investigations within the range of the genus have produced more or less sizeable collections of both demersal (Grieg, 1913; Le Danois, 1913) and planktonic stages (Petersen, 1919; Johansen, 1925; Russell, 1926-1940).

My interest in these fishes was aroused firstly by the difficulty experienced in separating the two species. After endeavouring to use the diagnoses of several authors, it was found possible to achieve this only on the basis of coloration. Then, while examining the testes of various gobies, it was noticed that no female *L. orca* were present in a collection of twenty two dissected individuals, and only immature males among twenty eight *L. scorpioides*. The possibility that the two so-called species were in fact based on sexual dimorphism in a single species indicated the need for taxonomic revision. Although such a view was put forward by Smitt (1900), this was not accompanied by any evidence and appears to have been overlooked by later authors. Dissection of the extensive material from the Irish Sea presented opportunities for settling the position of *Lebetus* among the gobioid families by osteological

study, and also for investigating various aspects of diet and reproduction. A preliminary account of some of this work has already been published (Miller, 1961b).

MATERIAL AND METHODS

The following specimens have been available for examination :

Isle of Man : 3 ♂♂, standard lengths 15.75–30.0 mm., including BMNH 1961.10.17.1, 3, 5, and one in PEM, and 27 ♀♀, 14.5–29.0 mm., inc. BMNH 1961.10.17.2, 4, and one in PEM.

Other British localities : 3 ♂♂, 12.0–30.0 mm., BMNH 88.3.22.9–10 part and BMNH 1903.4.14.4–7 part, and 2 ♀♀, 10.5 and 17.0 mm., BMNH 1903.4.14.4–7 part.

Scandinavia : 13 ♂♂, 13.5–26.0 mm., ZMO J3999 (type of *Gobius orca*), J4000, J4001, J4023 ; ZMB 771, 1887, 1893, 1966, 4174, 4175, 5294 ; ZMC 89, 91 ; and 4 ♀♀, 21.75–29.0 mm., ZMO J4020, J4021 (types of *G. scorpioides*) ; ZMB 536, 2009.

Abbreviations for museums are as follows :

BMNH	British Museum (Natural History).
PEM	Port Erin Marine Biological Station Museum.
ZMB	Zoologisk Museum, Universitetet i Bergen.
ZMC	Universitetets Zoologisk Museum, Copenhagen.
ZMO	Zoologisk Museum, Universitetet i Oslo.

The specimens were viewed by means of low power binocular and dissecting microscopes. With suitable illumination the sensory papillae were readily seen without staining after careful removal of mucus from the head and body surfaces. The skeleton was investigated by dissection of alizarin stained whole-mount preparations.

THE GENUS *LEBETUS* WINTHIER 1877

Lebetus Winther, 1877 : 49 (orthotype *Gobius scorpioides* Collett 1874) ; Smitt, 1900 : 554 ; Jordan, 1919 : 392 ; 1923 : 225 ; Duncker, 1928 : 140 ; Iljin, 1930 : 55 ; De Buen, 1930a : 123 ; 1930b : 5, 21 ; Koumans, 1931 : 43, 46 ; Whitley, 1931 : 155 ; De Buen, 1931 : 50, 54, 61 ; 1940 : 3 ; 1951 : 56, 57 ; Norman, MS : 413.

Lebistes Jordan, 1920 : 487 ; 1923 : 226 (*non* Filippi, 1862 : 69).

Butigobius Whitley, 1930 : 123.

Body moderately elongate, subcylindrical, with 25–29 ctenoid scales in lateral series. Head, nape, and back naked to origin of second dorsal fin, lacking skin folds or barbels. Postorbital length not more than half length of head. Anterior nostril a short tube. Opercle without scales. Preopercle and lower jaw unarmed. Branchiostegous membranes attached to sides of isthmus, but not fused across isthmus. Jaws oblique, subequal, maxillae ensheathed and not elongate. Teeth of both jaws in several rows, simple, erect. Tongue truncate to very weakly emarginate, free from floor of mouth anteriorly. Pelvic fins united along entire length, without anterior membrane (frenum) and with fourth branched ray somewhat produced. Pectoral girdle lacking flaps on anterior edge ; uppermost rays of pectoral fin not free from membrane. Dorsal fins separate, first dorsal with 6 rays, not pungent. Caudal fin rounded, not much longer than head.

Cephalic canals absent. Sensory papillae prominent but reduced in number. Two pairs of interorbital papillae (*p*). Cheek with only suborbital row *a*, a short longi-

tudinal row *c*, and an intermediate papilla; row *d* without posterior longitudinal section. Anterior dorsal (occipital) series (excluding *h*) in two groups of a few papillae. Opercular transverse row *ot* in two sections. Preoperculo-mandibular series in several parts.

In compiling his work on the genera of fishes, Jordan (1919, 1920, 1923) includes, together with *Lebetus* Winther 1877, the genus *Lebistes* Smitt 1899. Since Jordan gives "*L. scorpioides* Smitt" as the orthotype of this genus, the latter, as noted by Koumans (1931), is clearly an erroneous reference to *Lebetus* for which Smitt (actually 1900, not 1899) indicated *Gobius scorpioides* Collett as the type. The generic name *Lebistes* is preoccupied by *Lebistes* Filippi 1862 among the cyprinodont teleosts and, to replace this name within Jordan's list of gobiid genera, Whitley (1930) proposed *Butigobius* without consulting Smitt's paper. In a later account, Whitley (1931) unravels this confused story.

THE SPECIES OF THE GENUS

The present section embodies a review of the various characters proposed by earlier authors as being of value in the diagnosis of *L. orca* and *L. scorpioides*.

Coloration. The two species are reputed to differ in both body and fin coloration. The body of *Gobius orca* was described by Collett (1874, 1875a) as uniformly greyish except for darker areas between the second dorsal and anal fins, and at the root of the caudal fin, while that of *G. scorpioides* was said to possess four or five dark brown vertical bands across the sides. After examination of a living *scorpioides*, Winther (1877) remarked on the colourless caudal peduncle, and both Holt & Byrne (1903) and Le Danois (1913) emphasized the importance of this pale band, sharply demarcated anteriorly, as a means for the identification of *L. scorpioides*. In the original description, Collett (1874) mentioned that the second dorsal fin of *G. orca* had an indistinct white band in its outer half whereas the same fin in *G. scorpioides* showed only ill-defined banding. Alternate dark brown and snow white bands were found across the second dorsal fin of a later specimen of *G. orca* (Collett, 1885). Holt & Byrne (1903) regarded a superior black band to this fin as characteristic of *G. orca* and in their text referred to a row of white spots immediately below the dark periphery. These authors described and illustrated the second dorsal fin in *G. scorpioides* as banded with red, the markings in some cases being flanked by dark edging.

With the collection of *Lebetus* amassed for this work, it has been possible to segregate the individuals into two groups on the basis of differences in the coloration of the second dorsal fin. In the first of these, termed the *orca* group, the second dorsal fin has a thick black superior edge, below which occur white areas and wide oblique bands, yellow or ochre in life but grey in preserved material. Within the *scorpioides* group, the black edge to the second dorsal fin is present but much thinner and less intense than in the *orca* examples. The rest of the fin bears merely four narrow double lines of melanophores, enclosing in the living fish thin red or ferruginous striae, and separated by hyaline fin membrane. Among living *scorpioides*, madder brown lateral marks are pronounced on the body which, in *orca* fishes, is more uniform grey or yellowish grey although comparable markings may be quite prominent. A pale band on the caudal peduncle is more clearly defined in the *scorpioides* group, especially

when preserved, but living *orca* show this feature to a noticeable degree (cf. Pl. I and Text-fig. 3) and it is shown in Collett's illustrations of *Gobius orca* (1875a, 1885).

TABLE I.—*Relation of Coloration Groups to Sex and Maturity Stage*

Group	No. of males		No. of females all stages
	Mature and developing	Immature	
	(a) Dissected		
	<i>orca</i> . . .	21	
<i>scorpioides</i> . . .		6	22
(b) Not dissected			
<i>orca</i> . . .	16		
<i>scorpioides</i> . . .		5	11

The relation of these two colour patterns to sex and to gonad maturation is indicated in Table Ia, based on fifty Manx specimens whose sex and sexual development were confirmed by dissection. The sex and approximate maturity stage in a further thirty two British and Scandinavian examples have been determined by inspection of the genital papilla (Text-fig. 17), and these results are given in Table Ib. It is apparent that mature or developing male *scorpioides* do not occur, and that female *orca* are unknown at any stage of maturation. This distribution strongly implies that the *orca* coloration is the male livery of a species whose females and immature males bear the markings of *scorpioides*. Incipient development of the *orca* pattern in the second dorsal fin can, in fact, be noted among some of the immature males in the *scorpioides* group, which usually exhibit a pronounced black spot on the distal part of the first two interradian membranes of the second dorsal fin (see Le Danois, 1910, fig. 4). The above hypothesis is further supported by the range in standard length found in the three categories shown in Table II. The examples of *orca* are from 18.0–30.0 mm.

TABLE II.—*Standard Length Frequency in Coloration Groups, Expressed in 2 mm. Length Groups*

Coloration group	Standard length										
	10	12	14	16	18	20	22	24	26	28	30
<i>orca</i>					1	1	10	16	7	1	2
♂ <i>scorpioides</i> . . .		2	3	3		2	1				
♀ <i>scorpioides</i> . . .	1		1	2	1	2	5	9	5	7	

in length while male *scorpioides* do not exceed 23.0 mm. Tåning (1940) has reported juvenile *Lebetus orca* of 5–15 mm., but relied for the identification on meristic characters whose validity is doubtful. Female *scorpioides* attain about the same maximum length as that for *orca*.

The first dorsal fin in the *orca* individuals is a uniform yellowish grey edged with white, but in *scorpioides* is usually banded with a dark spot on the interradian membrane between the fifth and sixth rays. Confluence of these bands frequently occurs, and the spot may not be very distinct. This *scorpioides* group pattern is stated by

Holt & Byrne (1903) to be found only in the breeding male of "*Gobius scorpioides*". Fage (1918) regarded the presence of a black spot on the first dorsal fin of a 12.5 mm. example from the Dana collections as a sign of precocious development of supposed male coloration. However, in the material under consideration, the spot is well represented in adult females and among male *Lebetus* occurs only in the immature where it is not uncommonly absent. The single female *G. orca* mentioned in the literature was taken by Patience (1906) in the Firth of Clyde. This specimen has not been traced. The diagnosis of *G. orca* given by Patience was not derived from his own examples but seems to be a translation from Collett (1896) and could apply to individuals of either the *orca* or *scorpioides* group.

TABLE III.—*Meristic Characters Cited for Lebetus orca and L. scorpioides*

No. of fin rays					No. of Verte- brae	No. of Scales in l.l.	Authority
First dorsal	Second dorsal	Anal	Pectoral	Caudal			
<i>L. orca</i> ¹							
VI	11	10	18	3/13/3		28	Collett, 1874
VI	11	9	17	3/13/3		28	Collett, 1875a
VII	10-11	9	17	3/12-13/3		24	Collett, 1885
VII	I/9-10	I/8	17	12-13		25	Lilljeborg, 1884
VI-VII	I/9-10	I/8	17	x/13/x		c. 24	Smitt, 1892
VII	10-11	9	17	3/12-13/3			Collett, 1896
VI-VII	9-11	9-10				25-28	Holt & Byrne, 1903
VI-VII	I/9-10	18 (<i>sic</i>)	17-18	12-13		25-26	Duncker, 1928
VI-VII	I/9-10	I/8-9				24-28	De Buen, 1930a, b
VI-VII	10-12	8-10	18-20	7-8/11/6-7	28-29		Tåning, 1940
<i>L. scorpioides</i> ^{2, 3}							
VI	9	8	20 (18)	6/12/6		28	Collett, 1874
VI	9	8	18-20	6/12/6		28	Collett, 1875a
VI	9	8	c. 18	12		30	Winther, 1877
VI	I/8	I/7	18-20	12		28-30	Lilljeborg, 1884
VI	I/8	I/7	18-20	x/12/x		c. 28-30	Smitt, 1892
VI	9	8				28-30	Holt & Byrne, 1903
VI	9	7-8	18-20	x/12/x		28	Le Danois, 1910
VI	I/9	I/6				28	Le Danois, 1913
VI	I/8-9	I/6-9			27-28	28	Fage, 1918
VI	8-9	6-8			25-26		Petersen, 1919
V-VI	I/7-8	I/6-7	18-20	12	25-26	26-30	Duncker, 1928
VI	I/8-9	I/6-7	18-20	x/12/x		28-30	De Buen, 1930a, b, 1932

¹ Scales in l.l. c. 26-c. 28 (Grieg, 1913). ² Scales in l.l. 26, D₁ V (Collett, 1902). ³ Scales in l.l. 28 (Grieg, 1913).

Meristic characters. Radial formulae, vertebral and scale counts provided by various authors for the two species are shown in Table III. Although Collett originally ascribed 6 elements to the first dorsal fin of both species, he later changed this to

7 for *G. orca*. Lilljeborg (1884) and Smitt (1892) employed this supposed disparity in keys to Scandinavian gobies. *L. orca* is also regarded as having rather more articulated rays in the second dorsal and anal fins than *L. scorpioides*, and slight differences are indicated in pectoral and caudal fin ray counts. The number of scales along the lateral midline is reputed to be greater in *L. scorpioides* than in *L. orca*.

For the *orca* and *scorpioides* groups of the present material the meristic values in Table IV have been obtained. Methods of counting are described in the systematic section below. To minimise the effect of regional variation, results for British and Scandinavian collections have been kept separate. Mean values are given for the more numerous British material.

TABLE IV.—*Meristic Characters of Coloration Groups: Number of Observations (Highest in Bold Type) Against Value. M = Mean Value for British Material*

Coloration group	Origin of specimens												
	British Isles							Scandinavia					
	First dorsal fin rays												
	5	6	7					5	6	7			
<i>orca</i>		26							7	1			
<i>scorpioides</i>		34							6				
	Second dorsal fin articulated rays												
	6	7	8	9	10	11	M	8	9	10	11		
<i>orca</i>			1	18	7		9.23		5	3	1		
<i>scorpioides</i>	1	2	4	21	6		8.85		2	4	1		
	Anal fin articulated rays												
	5	6	7	8	9	M		5	6	7	8	9	
<i>orca</i>			1	19	6	7.19				5	4		
<i>scorpioides</i>	3	2	22	7		6.97		1		4	1		
	Pectoral fin rays												
	15	16	17	18	19	20	21	M	17	18	19	20	21
<i>orca</i>			2	15	20	15		18.92		7	4	2	
<i>scorpioides</i>	1	4	7	9	30	10	1	18.56			4	2	
	Caudal fin branched rays												
	8	9	10	11	M			8	9	10	11		
<i>orca</i>		24	1		9.04				5				
<i>scorpioides</i>	2	31	1		8.97				2				
	Scales in lateral series												
	25	26	27	28	29	M		25	26	27	28	29	
<i>orca</i>	2	18	10	6	2	26.68		1	3	2	1		
<i>scorpioides</i>	1	17	17	6	1	26.74			1	1	2		
	Vertebrae including urostyle (Manx specimens only)												
		26	27	28	29	M							
<i>orca</i>			2	13	1	27.94							
<i>scorpioides</i>			1	3	17	27.76							

Except for pectoral ray and scale counts in the Scandinavian fishes, where the number of observations is small, the most common value for each meristic character is the same in the two coloration groups and mean values are only slightly different. The wider range and somewhat lower means for fin ray counts in *scorpioides* are due

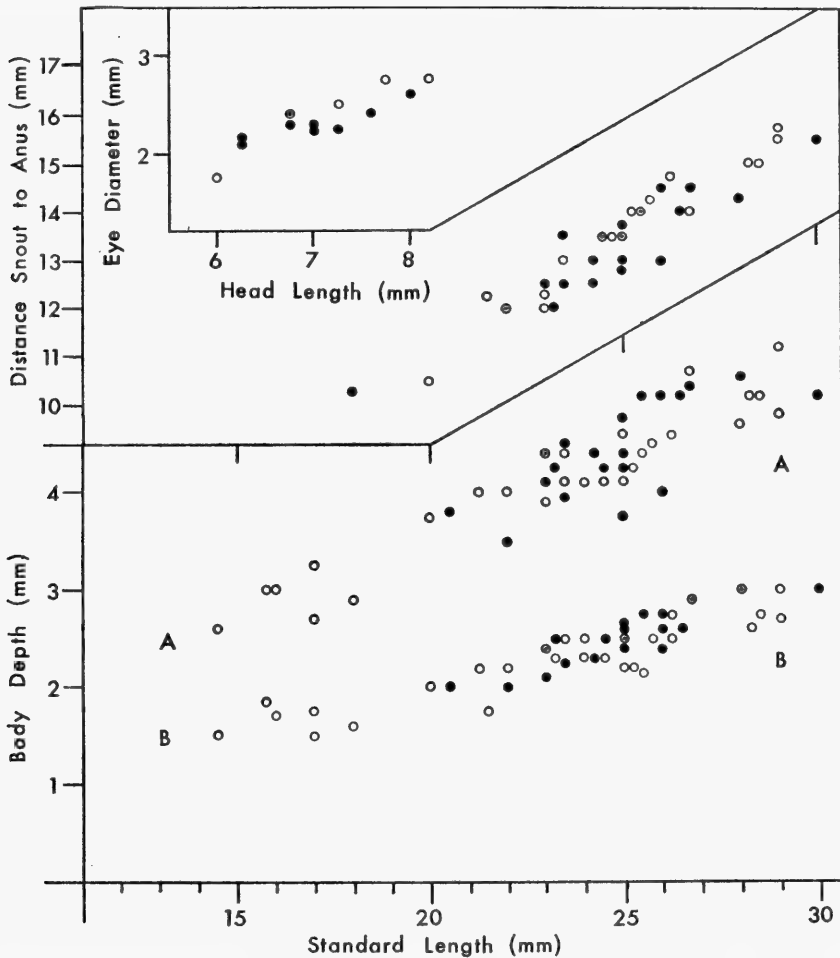


FIG. 1. Relation between standard length or head length and certain body measurements in the two coloration groups. A, body depth at origin of pelvic fin; B, depth of caudal peduncle before origin of caudal fin; ●, *orca*; ○, *scorpioides*; ◐, coincident points.

to the occurrence in this group of all the youngest and smallest individuals, among which such variation, as may be expected, is more pronounced (Barlow, 1961a). The specimen of *G. orca* (ZMO J4023) which prompted Collett (1885) to believe in a difference in first dorsal count between the two species has been examined and is the only individual among seventy-four examples of *Lebetus* to have seven first dorsal rays. Another fish, identified by Collett (1902) as *G. scorpioides*, was des-

cribed by this author as having only five first dorsal rays. This specimen (ZMB 536) has also been studied, and was found to possess an abnormal first dorsal fin (not included in Table IV) with only four rays, the first three of which are separated by an unusually large interspace from the last ray.

Body proportions. From their first description, *L. orca* has been held to be consistently slimmer than *L. scorpioides*. Collett (1874, 1875a) stated that body depth in the former was contained about seven times in the standard length, but only six times in *G. scorpioides*. Holt & Byrne (1903) noted that body depth was equal to one fifth and one sixth of the total length of *G. scorpioides* and *G. orca* respectively, and referred to this apparent difference in their key to the species. Other body proportions have been used in attempts at distinguishing these fishes. Collett (1875a), Lilljeborg (1884), Smitt (1892), and Holt & Byrne (1903) all regarded the eye to be relatively larger in the head in *G. orca* than in *G. scorpioides*. A supposed difference in the position of the anus with reference to the middle of the body was utilized in a key by Smitt (1892).

The significance of these characters has been tested in the present material and the results are given in Table V and Text-fig. 1. These show that the two coloration groups cannot be distinguished by such criteria.

TABLE V.—Mean and Range of Values for Certain Body Proportions in the Two Coloration Groups

Body proportions	Coloration group					
	<i>orca</i>			<i>scorpioides</i>		
	No. of Obs.	Mean	Range	No. of Obs.	Mean	Range
(a) In standard length						
Depth at origin of pelvic fin	21	5.64	5.10-6.65	28	5.65	5.10-6.30
Depth at origin of anal fin	23	6.50	5.90-7.30	26	6.55	5.70-7.50
Depth (least) of caudal peduncle before caudal fin origin	23	10.00	9.20-11.0	29	10.22	8.50-12.30
Distance from snout to anus	22	1.87	1.75-2.00	18	1.85	1.75-1.90
(b) In head length						
Diameter of eye	8	3.02	2.80-3.20	5	2.98	2.80-3.40

Development of the dorsal fins. Collett (1874, 1875a) reported that the first dorsal fin was considerably higher than the body in *G. orca*, but only slightly so in *G. scorpioides*. It was also stated that the first rays of the fin were produced and free from the interradyal membrane in *G. orca*. Duncker (1928) treated the latter as a feature of diagnostic value, and believed that *L. orca* differed from *L. scorpioides* in having the first dorsal fin higher than the second dorsal fin.

In the present work, fin ray length has been used as an index of fin height because the latter is difficult to measure accurately. With adults in both the *orca* and *scorpioides* groups, the second and third rays of the first dorsal fin were longer than any in the second dorsal fin, and greater than the body depth at the origin of the pelvic

fin. In length of the second ray, there was little difference between the groups (Text-fig. 2A), while for the third ray and the other rays of the first dorsal fin, as well as in the second dorsal fin, there is a more or less pronounced divergence, *orca* specimens having the longer rays. This trend is very noticeable in the last three rays of the first dorsal fin (Text-fig. 2B) and, together with corresponding growth of the interradial and posterior membranes, gives the fin a much greater spread in the *orca*

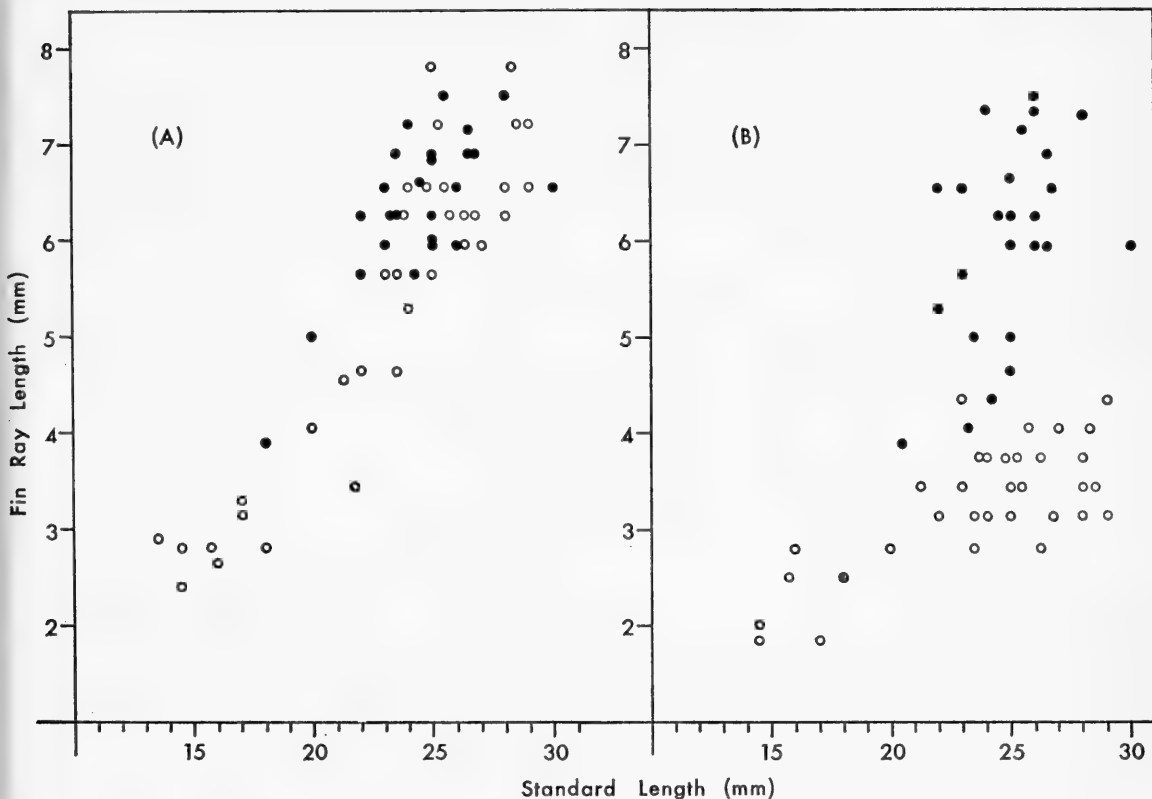


FIG. 2. Relation between standard length and lengths of certain first dorsal fin rays in the two coloration groups. (A) Second ray; (B) Fifth ray. Other symbols as Fig. 1.

individuals. In the best preserved specimens of both groups, the tips of the dorsal fin rays do not project beyond the fin membrane.

Other morphological characters. Comparison of other body proportions and anatomical features, such as patterns of sensory papillae over the head and body, does not reveal any differences between the *orca* and *scorpioides* groups.

Distribution. The two species have been recorded throughout the geographical range of the genus, which is eastern Atlantic boreal in occurrence. Thus *L. orca* and *L. scorpioides* are both reported from Iceland (Saemundsson, 1926; Tåning, 1940) and the western coast of Norway (records summarized by Grieg, 1913). In the south, they are known from the Gulf of Gascony (Collett, 1896) and Roscoff (Le Danois,

1910) respectively. It is only in Danish waters and in the western Channel, where most records are of juvenile specimens, that many individuals of one species (*L. scorpioides*) have been obtained and none of the other.

A slight divergence in habitat preference was implied by Duncker (1928) who mentioned that *L. orca* occurred on "fine to coarse sandy ground" while *L. scorpioides* inhabited "mostly hard ground (*Lithothamnion*, shelly sand, gravel)". Tåning (1940) suggested that *L. orca* was a more offshore form than *L. scorpioides*, but Le Danois (1948) listed both gobies as occurring in the "zone subcôtière" (40–100 m.) and deeper parts (120–200 m.) of the continental shelf. While investigating the bottom fauna off the south of the Isle of Man, Jones (1951) encountered both *Lebetus* species on the coarser offshore grounds. The records of *L. orca* were restricted to an area of several square miles south west of the Calf Island, where the bottom is overlaid by a deposit of dead shells, chiefly *Glycimeris*. Both species were obtained by Grieg (1913) from similar bottoms in Hardangerfjord, Norway. The positions of capture for the Manx specimens collected by Jones and later workers have been plotted in Text-fig. 15, where the number of *orca* and *scorpioides* specimens are indicated by symbol at each locality from which fishes have been examined in the present work. No ecological separation is demonstrable between the two groups and, at localities where adequate material has been obtained, both *orca* and *scorpioides* appear to be represented in comparable numbers.

The bathymetric range off the Isle of Man is 18–64 m. for the *orca* group, and c. 18–64 m. for *scorpioides*. Previous authors have cited depth ranges of 20–375 m. and 3·5–135 m. for *L. orca* and *L. scorpioides* respectively (Holt & Byrne, 1903; Grieg, 1913). The apparently greater penetration of deeper waters by the former species may well be due merely to lack of collecting. Pronounced contrast in bathymetric distribution between the two species remains to be established.

Conclusion. The above paragraphs indicate that the two groups to which *Lebetus* specimens may be assigned are obviously different only in coloration and in growth of the dorsal fins, especially the first. The *orca* group consists entirely of males, almost all maturing or mature, and the *scorpioides* of females and immature males. The type specimens of *Gobius orca* (ZMO J3999) and *G. scorpioides* (ZMO J4020, J4021) have been available for study, and are a male, maturing if not mature, and two females respectively. Sexual dimorphism in colour and fin ray length is a well known phenomenon among many teleosts, and has recently been discussed by Egami (1960) for Japanese gobies. It appears safe to conclude, therefore, that the two names apply to one and the same species, for which the name *orca* Collett 1874, p. 446, ranks by page priority as the senior synonym to *scorpioides* Collett 1874, p. 447.

Lebetus orca (COLLETT 1874)

(Text-figs. 3 and 4)

Gobius orca Collett, 1874: 446; 1875a: 172, pl. III, figs. 1–3; 1875b: 57; Winther, 1877: 49; Lilljeborg, 1884: 616; Smitt, 1892: 259, fig. 66; 1900: 554; Collett, 1902: 57; Holt & Byrne, 1903: 57, fig. 5; Patience, 1906: 74; Grieg, 1913: 41; Jenkins, 1925: 88, 97; Elmhirst, 1926: 154; Koumans, 1931: 47; Whitley, 1931: 155; Lönnberg &

- Gustafson, 1935: 246, fig. 2 (photograph); Norman, 1935: 58; Jenkins, 1936: 88, 97, 388; Ehrenbaum, 1936: 168, fig. 147; Andersson, 1942: 85; Jones, 1949: 28.
- Gobius scorpioides* Collett, 1874: 447; 1875a: 175, pl. III, figs. 4-6; 1875b: 58; Lilljeborg, 1884: 620; Smitt, 1892: 260, fig. 67; Holt & Byrne, 1898: 337; Grieg, 1899: 7; Smitt, 1900: 554; Collett, 1902: 59; Holt & Byrne, 1903: 56, pl. II, figs. 2 and 3; Aflalo, 1904: 158; Holt & Byrne, 1910: 7; Crawshaw, 1912: 300, 385; Farran, 1912: 2, 3; Otterstrøm, 1912: 162; Grieg, 1913: 43; Clark, 1914: 372; Petersen, 1917: 10, 13, 14; Fage, 1918: 63, 71, 101, figs. 54-56; Jordan, 1919: 392; Jenkins, 1925: 88, 96, pl. 30, figs. 2 and 3; Johansen, 1925: 5, 6, 10, fig. 6; Saemundsson, 1926: 178; 1927: 19; Koumans, 1931: 43, 46; Whitley, 1931: 155, 156; Lönnberg & Gustafson, 1935: 247; Norman, 1935: 58; Jenkins, 1936: 88, 96, 388, pl. 30, figs. 2 and 3; Ehrenbaum, 1936: 168; Andersson, 1942: 85; Jones, 1949: 28; Went, 1957: 18.

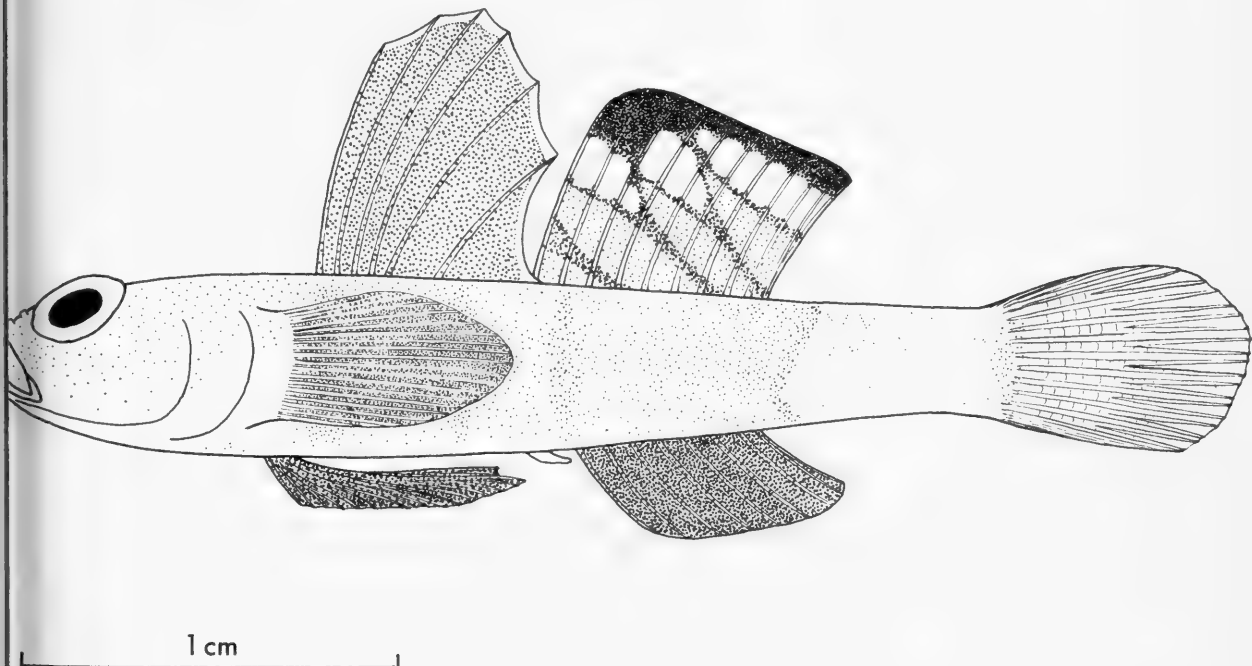


FIG. 3. *Lebetus orca* (Collett), mature male.

- Lebetus scorpioides* Winther, 1877: 49; Malm, 1877: 651; Winther, 1879: 18; Petersen, 1919: 48, 49, 55, 59, 61, pl. I, figs. 27-29, pl. III, fig. 4; Clark, 1920: 226, 232; Russell, 1926a: 134, 152-153, 155-157; 1926b: 397, 411; Duncker, 1928: 141, fig. 13; Ehrenbaum *et al.*, 1929: 155; Iljin, 1930: 55, fig. 43; De Buen, 1930a: 125; 1930b: 6, 21, 27, figs. 9 and 10; Russell, 1930a: 661, 672; 1930b: 708, 713, 718; De Buen, 1931: 50; Marine Biological Association, 1931: 324; De Buen, 1932: pl. 300; Russell, 1935: 153, 154; 1936: 604; 1939: 386; Bal, 1940a: 82, 86; 1940b: 16; Russell, 1940: 270; Tåning, 1940: 279; Brunn & Pfaff, 1950: 50; Jones, 1950: 31; 1951: 137, 144; Cantacuzene, 1956: 41; Marine Biological Association, 1957: 401.
- Lebetus orca* Collett, 1885: 61, pl. I, figs. 1 and 2; 1896: 41; Duncker, 1928: 142, fig. 14; De Buen, 1930a: 125; 1930b: 21, 23, 27; 1931: 50; Tåning, 1940: 277, 282; Saemundsson, 1949: 38, 136; Bruun & Pfaff, 1950: 50; Jones, 1950: 31; 1951: 137, 144.
- Gobius jeffreysii* Günther, 1888: 210 (*partim*), pl. III, fig. 3 (*non* Günther, 1867: 290, pl. V, fig. c).

Gobius (Lebetus) scorpioides Smitt, 1900 : 554 ; Le Danois, 1910 : 168, figs. 4 and 5 ; 1948 : 279 ; 953 : 136 and facing pl., 184.

Gobius (Lebetus) scorpioides guiletti Le Danois, 1913 : 91, 160, 161, 169, 186, 189, figs. 159-161.

Gobius (Lebetus) orca Le Danois, 1948 : 121, 279.

Gobius sp. Schmidt, 1904 : 53 ; Saemundsson, 1908 : 32.

TYPE SPECIMENS. The holotype of *Gobius orca* (ZMO J3999) is a male from Espevaer, Hardangerfjord, Norway, dredged in 145-180 m. during July 1873. The two syntypes of *Gobius scorpioides* (ZMO J4020, J4021) are females from Hvittingsô, Stavangerfjord, and Lyngholmen, Hardangerfjord, dredged in 37 and 110 m., during July 1872 and August 1873 respectively. In condition, these specimens are now somewhat shrunken, and the caudal fin in each one has been cut off by an earlier investi-

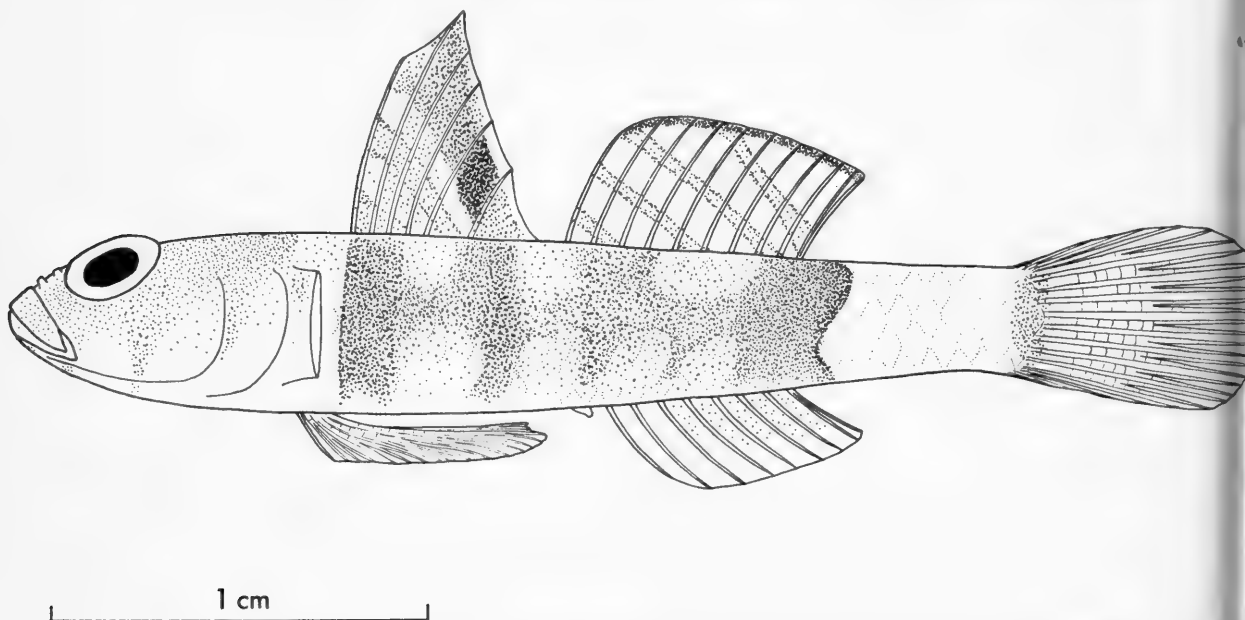


FIG. 4. *Lebetus orca* (Collett), mature female. Pectoral fin removed to show body markings.

gator. Present lengths, original lengths (Collett, 1874, 1875a) and meristic values are given in Table VI.

TABLE VI.—*Present Lengths, Original Lengths (Collett, 1874, 1875a, b) and Meristic Values for Type Specimens of Gobius orca and G. scorpioides.* d = *Damaged*

Sex	ZMO No.	Lengths (mm.)		Meristic values				
		Original standard + Caudal fin	Present standard	First Dorsal	Second dorsal	Anal	Pect- oral	Scales in l.l.
♂	J 3999	26.0+6.0	25.0	d.	I/10	I/8	d.	26-27
♀	J 4020	total 28.0	21.5	VI	I/9	I/7	d.	d.
♀	J 4021	30.0+7.0	29.0	VI	I/9	I/7	20	27-28

GENERAL DESCRIPTION. Body subcylindrical, laterally compressed towards caudal fin; in standard length, depth at origin of pelvic fin 5.1-6.65 (mean 5.65), at origin of anal fin 5.7-7.5 (6.53), of caudal peduncle before origin of caudal fin 8.5-12.3 (10.12). Head rounded; in standard length, horizontal length (snout to upper origin of opercle) 3.2-4.1 (3.71), maximum width (between upper origins of opercles) 5.25-5.95 (5.68). Horizontal distance from tip of snout to origin of first dorsal fin 2.7-3.05 (2.9), to origin of second dorsal fin 1.7-1.9 (1.81), to anus 1.75-1.95 (1.86), to origin of anal fin 1.6-1.75 (1.69), to origin of pelvic fin 3.2-4.0 (3.47), all in standard length. Caudal peduncle (end of anal fin base to origin of caudal fin) horizontal length 4.15-5.1 (4.71) in standard length, depth 1.8-2.35 (2.07) in own length. In head length, snout 3.8-5.6 (4.7), eye 2.8-3.4 (3.0), postorbital length 2.0-2.7 (2.34), cheek 3.8-4.85 (4.34); eye and cheek direct, rest horizontal measurement. Interorbital minimum width (bony) 4.3-7.4 (5.5) in eye length. Snout less than diameter of eye, with moderately sloping profile; nostrils adjacent, anterior on short tube, not projecting over upper lip and with entire distal rim lacking local prolongation; posterior nostril also tubular but shorter. Eyes large, close together. Postorbital region never exceeding half head length; profile more or less flat, without dermal ridges. Upper jaw relatively wide, about equal to preorbital area. Mouth oblique, lower jaw at most only slightly in advance of upper; maxilla ends posteriorly under anterior quarter of eye. Lower jaw unarmed, without barbels. Cheek smooth, without dermal ridges. Preopercle unarmed. Branchiostegous membrane attached to entire lateral margin of isthmus from immediately anterior to lower edge of pectoral lobe and without transverse fusion across isthmus (Text-fig. 5). Teeth simple, caniniform, erect in both jaws. Dentition of jaws an outer row of larger teeth with narrow band of two to four rows of smaller teeth. Pharyngeal teeth relatively large, recurved, in two superior and one inferior median patch (see description of skeleton). Tongue more or less truncate, with anterior edge rounded laterally; at most pronounced, a very slight median emargination (Text-fig. 6B). Gill rakers small protuberances, not spinous, about 6-8 on first arch. Sagittal otolith rectangular, anterior and posterior edges slightly concave, inferior edge slightly convex, superior edge with angular projection near posterior end; outer surface convex, more flattened in middle, inner surface convex, with furrow in middle and shallower groove to posterior edge (Text-fig. 6A).

FINS. In the following counts, spinous elements are represented by large roman, articulated rays by arabic numerals. The terminal bifid ray in the second dorsal and anal fins is counted as one element. Only in the caudal and pelvic fins are articulated rays branched. The range of values is given in parentheses after the most common number, frequency distribution being shown in Table VII.

First dorsal fin VI (VI-VII); second dorsal fin I/9 (6-11); anal fin I/7 (5-8); caudal fin (branched rays) 9 (8-10); pectoral fin 19 (15-21), pelvic fin I/5 + I/5. In standard length, first dorsal base 7.95-8.95 (8.24), second dorsal base 3.75-4.55 (4.24), anal base 4.85-5.8 (5.4), longest caudal ray 3.2-4.45 (for standard lengths up to 20.0 mm., mean = 3.55; more than 20.0 mm., mean = 3.92), longest pectoral ray 3.7-4.45 (4.0), pelvic origin to tip of fifth pelvic articulated ray 3.85-4.55 (S.L. up to 25 mm., mean = 4.05; more than 25.0 mm., mean = 4.2). First dorsal fin

TABLE VII.—*Meristic Characters of Lebetus orca: Number of Observations against Value*

Locality		First dorsal fin rays						
		5	6	7				
British Isles	.	60						
Scandinavia	.	13				1		
		Second dorsal fin articulated rays						
		6	7	8	9	10	11	
British Isles	.	1	2	5	39	13		
Scandinavia	.	2			9	4	1	
		Anal fin articulated rays						
		5	6	7	8	9		
British Isles	.	3	3	41	13			
Scandinavia	.	1		9	5			
		Pectoral fin rays						
		15	16	17	18	19	20	21
British Isles	.	1	4	9	24	50	25	1
Scandinavia	.					7	8	4
		Caudal fin branched rays						
		8	9	10	11			
British Isles	.	2	55	2				
Scandinavia	.	7						
		Scales in lateral series						
		25	26	27	28	29		
British Isles	.	3	35	27	12	3		
Scandinavia	.	1	4	3	3			
		Vertebrae including urostyle						
		26	27	28	29			
Isle of Man	.	1	5	30	1			

TABLE VIII.—*Dorsal Fin Ray Lengths Expressed in Standard Length for Mature and Immature Lebetus orca*

		First dorsal fin						Second dorsal fin	
		I	II	III	IV	V	VI	I	I
Mature ♂♂ .	.	3.85-	3.40-	3.35-	3.20-	3.25-	4.15-	4.35-	4.10-
	.	5.20	4.35	3.95	3.95	4.70	5.90	5.80	4.90
Mature ♀♀ .	.	4.95-	3.20-	3.95-	5.40-	6.35-	9.50-	6.40-	5.75-
	.	6.50	4.50	5.30	7.25	9.35	13.50 (21.0)	8.25	7.05
Immature ♂♂ .	.	4.65-	3.65-	4.00-	4.95-	5.30-	7.25-	6.05-	5.90-
	.	6.80	6.05	6.05	6.80	9.10	13.60	9.20	7.25
Immature ♀♀ .	.	6.05-	4.15-	4.45-	5.40-	7.00-	11.00-	6.80-	5.40-
	.	9.35	6.40	5.80	7.15	8.50	14.40	8.50	7.00

commences behind vertical of pelvic origin, last ray arising well before vertical of anus. In standard length, dorsal fin ray lengths as in Table VIII (see also Text-figs. 19 and 20). None of dorsal rays prolonged beyond interradiat membrane. In most males, no dorsal interspace, posterior membrane of first dorsal reaching origin of second dorsal fin, sometimes extending to one side of first element of latter. In females and some immature males, a short dorsal interspace. Second dorsal fin begins over or just behind vertical of anus, finishes opposite posterior end of anal fin. Anal fin commences below first elements of second dorsal fin, and ends below last element of latter. In standard length, spinous ray 8.75–10.4 (males), 10.45–12.85 (females); first articulated ray

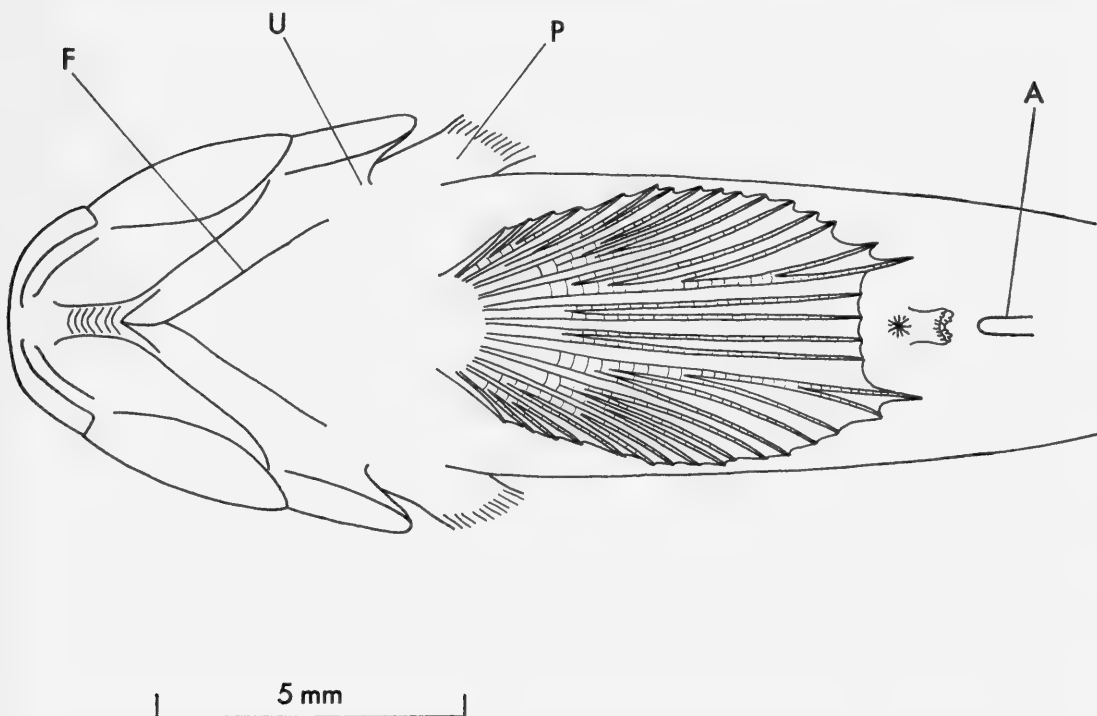


FIG. 5. Ventral view of female *L. orca*. F, fold of attached branchiostegous membrane; U, origin of branchiostegous attachment to isthmus; P, pectoral fin; A, anal fin.

6.65–8.95 (males), 8.2–10.7 (females); penultimate ray 7.1–9.7 (males), 9.2–12.45 (females). Caudal fin with rounded margin, convex posteriorly. Pectoral fin extends back to opposite anus; uppermost pectoral rays not separated from fin membrane; no dermal flaps on anterior edge of pectoral girdle. Pelvic fins not adnate, completely united along their length but with anterior membrane between spinous rays entirely absent; fourth articulated ray somewhat prolonged, terminating lateral to anus or genital papilla, but fifth ray ending immediately before anus (Text-fig. 5).

SCALES. Behind vertical of anus, body covered with large imbricating ctenoid scales; anteriorly, ctenoid scales present in narrow belt on lateral midline forward

to axilla. Lateral series 26–27 (25–29), transverse series (anterior end of second dorsal backwards to anal fin) 7 (see Table VII). Scales absent from head, predorsal region, upper part of body lateral to first dorsal and origin of second dorsal fin, pectoral lobe, axilla, isthmus, breast, and abdomen. Midline scales of caudal peduncle hexagonal,

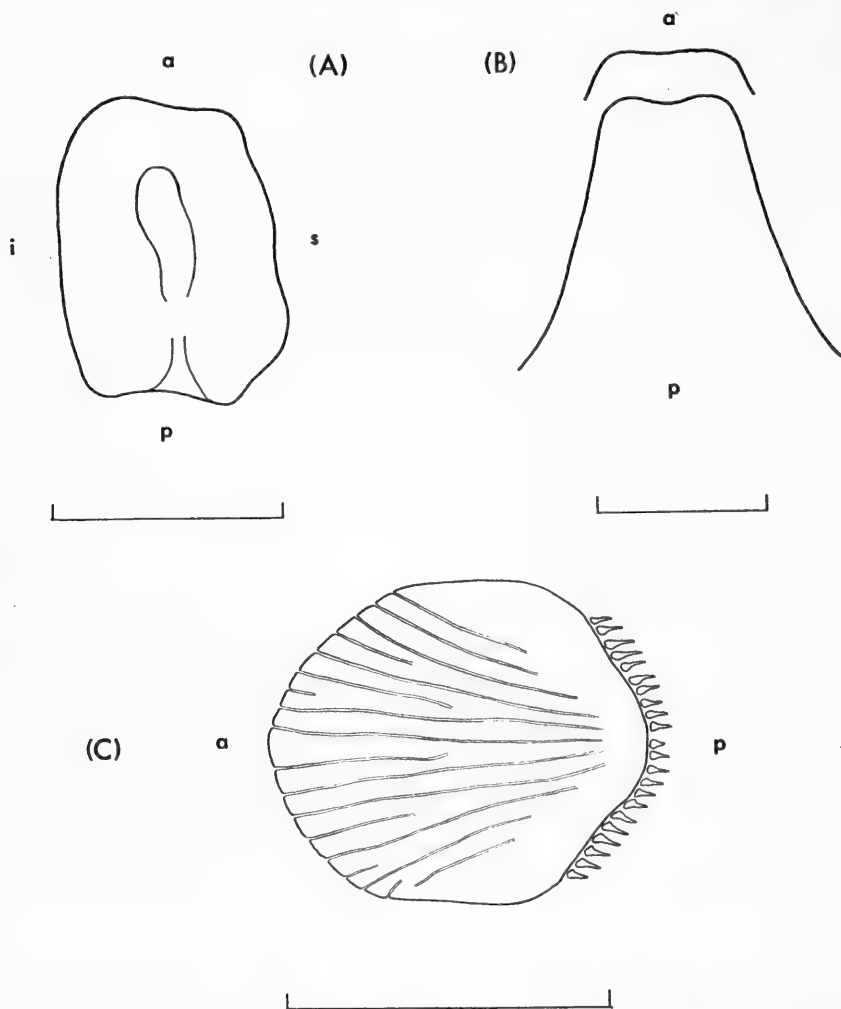


FIG. 6. *L. orca*: (A) Sagittal otolith, median view, (B) Tongue, showing extremes of variation in shape of anterior edge. (C) Scale from caudal peduncle (sclerites omitted). a, anterior; p, posterior; s, superior; i, inferior. Scale with each figure 1 mm.

somewhat elongate, with about 20 ctenii (Text-fig. 6c); scales at base of caudal fin without elongate lateral ctenii.

VERTEBRAE. Usually 28 (26–29), including urostyle (Table VII).

COLORATION. Basic pattern of more or less well developed vertical bars; first and widest below anterior part of first dorsal fin, second below posterior end of first

dorsal, third below anterior end of second dorsal, and fourth a curved mark across caudal peduncle posterior to termination of second dorsal and anal fins. Bars tend to be connected along lateral midline by denser pigment but, nearer dorsal and ventral edges of body, are separated by paler areas. Caudal peduncle from fourth bar to origin of caudal fin almost colourless with some pale yellowish or ferruginous mottling in life; a vertical dark mark across origin of caudal fin.

(a) Mature male (Text-fig. 3 and Pl. I). Body yellowish or more dusky grey; bars greyish, somewhat less well marked than in female, (especially after preservation, c.f. Text-fig. 3 and Pl. I) but posterior edge of caudal peduncle bar clearly defined in life and caudal peduncle more or less colourless. Head yellowish to reddish grey above; underside of head, cheeks, isthmus, and breast suffused with reddish orange. First dorsal fin dusky yellow, edged with white. Second dorsal fin with intense black edge, especially wide anteriorly on distal part of first two interradi al membranes, and broad oblique yellow bands separated from edge and one another by white bands, which, excepting posterior band, usually become narrower and greyish towards base of fin (wide bands to base of second dorsal shown in Pl. I are exceptional). Anal fin dusky, without white edge. Pectoral and pelvic fins dark; pectoral suffused with orange red proximally, being most intense over bases of lower pectoral rays. Caudal fin usually clear, or with traces of yellow or red.

(b) Mature female (Text-fig. 4). Body pale brown; vertical bars conspicuous purplish brown with anterior edge of first and posterior edge of caudal peduncle bar sharply defined; fusion and irregularity of intermediate bars may produce effect of coarse mottling, and sometimes a pale transverse band lies across origin of first dorsal fin between level of pectoral bases and anterior edge of first vertical bar. Head pale brown, reddish or ferruginous above; reddish brown vertical marks across cheek and immediately behind preopercle; red striae on underside of head across mental region, at angle of jaw, and below eye. First dorsal fin with oblique yellow to orange red bands each bordered with black and tending to coalesce across middle interradi al membranes; uppermost band wider, darkening posteriorly to form more or less well defined spot on distal part of last interradi al membrane; edge of fin membrane may be whitened especially adjacent to spot. Second dorsal fin with narrow dark edge, and four narrow oblique bands of orange red, each bordered with black, across hyaline fin. Caudal, pectoral, and pelvic fins usually hyaline; a reddish brown mark on upper part of pectoral lobe. Anal fin pigmented on proximal areas of posterior interradi al membranes.

(c) Immature fishes. Both sexes resemble mature female. First dorsal fin of males usually more uniform in colour but may show bands and spot; second dorsal fin with conspicuous dark spot at distal end of first and second interradi al membranes, as well as rather wider oblique bands and more intense dark edge. In youngest individuals, pelvic and anal fins black, and dark vertical bar across pectoral fin; underside of head, isthmus, and breast covered with melanophores, which later disappear.

LATERAL LINE SYSTEM. Terminology and lettering of the sensory papillae in the present text and diagrams follow the system invented by Sanzo (1911). As part of the general reduction in number of papillae, in certain cases only one or at most a

few papillae occur in areas where a well defined row or rows are found in the genera described by Sanzo. Under these circumstances, it is not possible to be sure of the exact homologies of the papillae in *Lebetus* so that in some instances composite lettering has been adopted.

(a) Cephalic canals. These are absent.

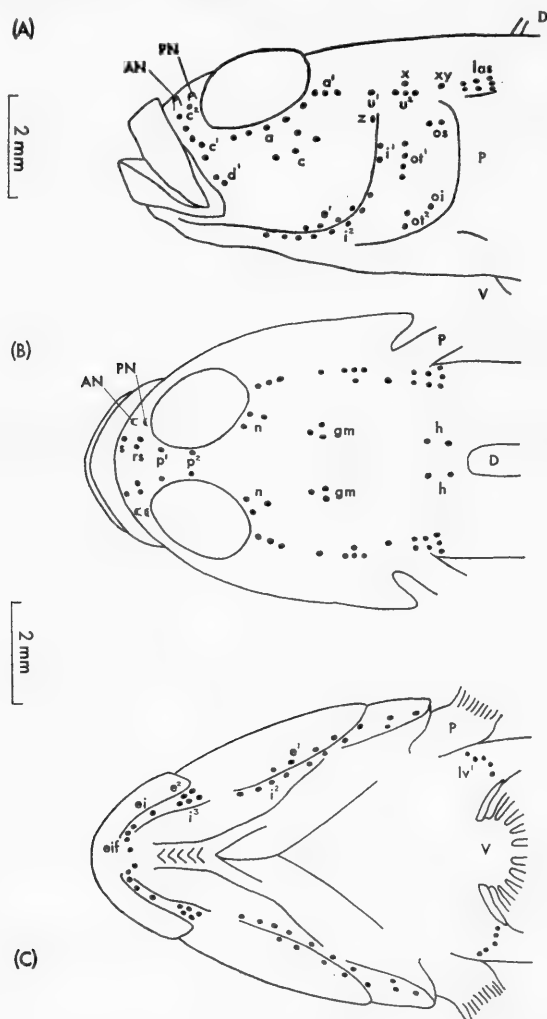


FIG. 7. Sensory papillae of head in *L. orca*. (A) Lateral, (B) Dorsal, (C) Ventral views. AN, anterior nostril; PN, posterior nostril; D, first dorsal fin; P, pectoral fin; v, pelvic fin. Other abbreviations as in text.

(b) Sensory papillae. Relatively large, and easily seen. Numbers of papillae are given in parentheses.

(i) Preorbital (Text-figs. 7A, 7B). Median series in two parts, anterior s (1) and posteriorly rs (2, inner sometimes absent); another papilla rarely present between

r_s and p^1 of interorbital series. Lateral series c^1 (5) and c^2 (1), the latter rarely present.

(ii) Suborbital (Text-fig. 7A). Infraorbital row a (5) continued as a^1 (3) into oculo-scapular groove. Longitudinal row c (2-3, rarely 4). Between rows a and c a single papilla, probably referable to c . Row b absent. Row d represented by d^1 (2), without horizontal posterior section.

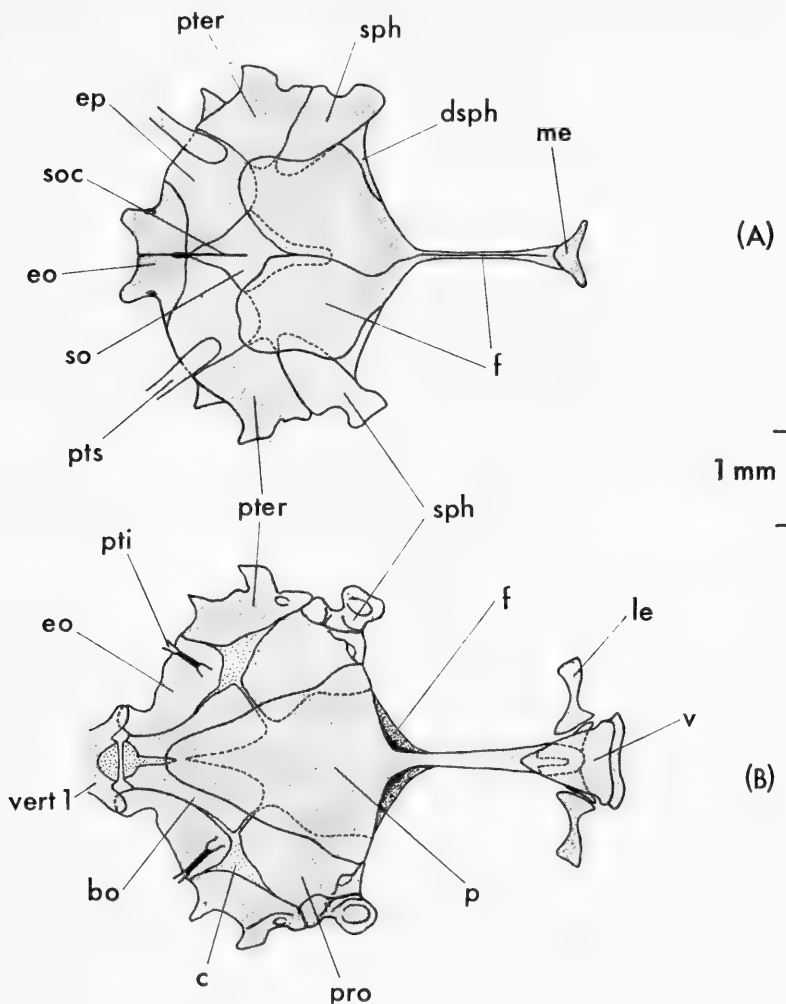


FIG. 8. Neurocranium of *L. orca*. (A) Dorsal, (B) Ventral views. Abbreviations as in text.

(iii) Preoperculo-mandibular (Text-figs. 7A, 7C). External row e in two parts, posterior e^1 (3-4, rarely 5), and anterior e^2 (2-3). Internal row i in three parts; superior i^1 (2), posterior i^2 (7-8), and anterior i^3 (2-3). A single papilla ei usually present halfway between angle of jaw and mental region. Mental row eif (2-4).

(iv) Oculoscapular (Text-fig. 7A). Longitudinal row u of oculoscapular groove in two parts, anterior u^1 (1), and posterior u^2 (3). One papilla z anterior to commence-

ment of preopercular groove, another x over u^2 , and a third xy above border of opercle. Axillary series las in three vertical rows (2; 2; and 2-3, rarely 4, respectively).

(v) Opercular (Text-fig. 7A). Transverse row ot in two parts, upper ot^1 (4, very rarely 5) and lower ot^2 (2); superior longitudinal row os (2); and inferior longitudinal row oi (1).

(vi) Anterior dorsal (occipital) (Text-fig. 7B). Three groups, anterior n (3, rarely 4), middle gm (3), and posterior h (2).

(vii) Interorbital (Text-fig. 7B). Two papillae, anterior p^1 and posterior p^2 ; former occasionally absent.

(viii) Trunk (not illustrated except lv^1). Three series; superior with ld^1 (1-2) flanking first dorsal fin near origin, ld^2 (2) near posterior membrane of first dorsal fin, and ld^3 (3) on caudal peduncle near origin of caudal fin; median with about nine or ten short transverse rows ltm^1 to ltm^9 or 10 (first usually 4, rest 3 each) along midline to origin of caudal fin; inferior with lv^1 (4-8) between origins of pelvic and pectoral fins (Text-fig. 7C), lv^2 of one, rarely two, lateroventral rows on abdomen (3-4 each), and lv^3 (2) just before anus.

(ix) Caudal (not illustrated). Three papillae around posterior edge of last scale of midline which overlaps base of caudal fin, and up to 12 papillae, from middle papilla of former group, in line on interradiial membrane to near posterior edge of fin. Sometimes a parallel series on membrane below.

SKELETON. This is well ossified.

(a) Neurocranium (Text-figs. 8, 9). (i) Proportions. Postorbital region broad, slightly wider than long, depressed; interorbital septum strongly compressed especially in dorsal aspect; preorbital region small.

(ii) Occipital bones. Basioccipital (bo) with broad forks truncate anteriorly, articulating posteriorly with centrum of first vertebra (*vert.* 1). Exoccipital (eo) carrying posteriorly stout articular process opposed to upper surface of prezygapophysis of first vertebra, extending ventrally along side of skull with knob near distal end to which inferior limb (pti) of posttemporal is attached by strong ligament, and dorsally in contact with fellow behind supraoccipital. Supraoccipital (so) relatively large, diamond shaped, bearing prominent crest (soc), which is triangular with emarginate posterior edge and pointed apex and continues backwards on to anterior part of exoccipital area.

(iii) Otic bones. Sphenotic (sph) at anterior corner of neurocranium produced into horizontal flange for articulating with hyomandibular, and with wide posterior extension separated from epiotic; a dermosphenotic element ($dsph$) forms part of posterior border of orbit, firmly attached to sphenotic proper. Pterotic ($pter$) forming posterior corner of neurocranium with articular surface on ventral face for hyomandibular. Epiotic (ep) large, in contact with superior limb (pts) of posttemporal, approaching fellow in dorsal midline but separated by posterior end of supraoccipital. Prootic (pro) broad, meeting basioccipital. No opisthotic, but on ventral surface of neurocranium, a cartilaginous area (c) bounded by prootic, pterotic, exoccipital, and to a slight extent by basioccipital.

(iv) Preorbital neurocranium. Mesethmoid (me) with cartilaginous body, ossified

as posterior vertical lamina at anterior corner of interorbital space surmounted by triangular ossification, from whose anterior end a thin, dorsally concave plate extends forwards over cartilage towards vomer, and with lateral ossified area adjacent to lateral ethmoid. Vomer (*v*) consisting of well ossified transverse bar across anterior end of ethmoid cartilage with thin scale of bone extending backwards over ventral surface of ethmoidal region and end of parasphenoid. Lateral ethmoid (*le*) attached to side of ethmoid cartilage; proximal part of upper surface and adjacent mesethmoid forming articular surface for ethmoidal head of palatine, and, laterally, alate in border of orbit. Prefrontal (*pf*) falciform, attached to anterior face of lateral ethmoid wing and distally related to maxilla.

(v) Other dermal bones. Frontal (*f*) large, overlapping sphenotic, pterotic, epiotic, and supraoccipital, ending anteriorly below posterior edge of mesethmoid. No parietal. Parasphenoid (*p*) large triangular plate covering edges of basioccipital

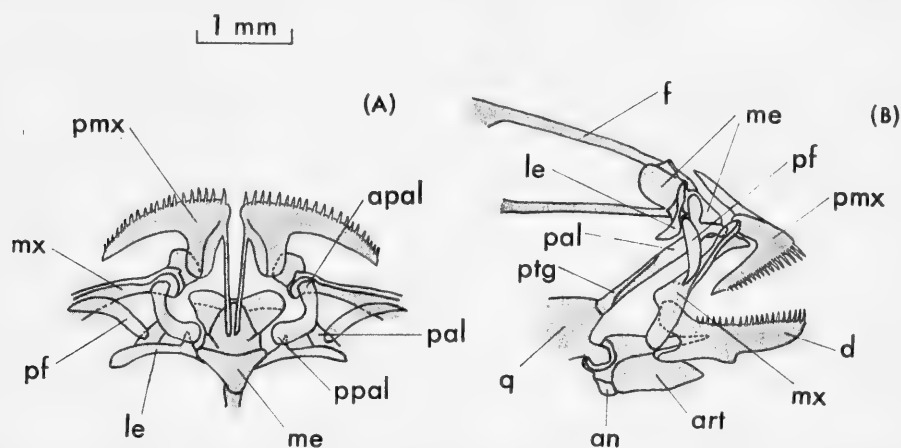


FIG. 9. Preorbital cranium of *L. orca*. (A) Dorsal, (B) Lateral views. Abbreviations as in text. Note that only outer row of teeth is shown on premaxilla and dentary.

and prootic with anterior process terminating below mesethmoid and above vomer. Between orbits, frontals and parasphenoid much compressed, forming upper and lower boundaries of interorbital septum, which is otherwise unossified save for mesethmoid lamina. Nasals and suborbitals absent.

(b) Branchiocranium (Text-figs. 9, 10, 11). (i) Suspensorium. Hyomandibular (*h*) broad, with two heads; anterior head articulating with lateral flange of sphenotic, posterior head with anterior end of ventral face of pterotic; posteriorly, strong stay on inner face articulating with operculum; posteroventrally, sword-shaped process extends over upper end of preoperculum. Symplectic (*sy*) a slender bone running along lower anterior corner of hyomandibular to inner surface of quadrate almost to angle of jaw. Metapterygoid (*mpt*) elongate, along anterior edge of hyomandibular and symplectic but not reaching quadrate. Quadrate (*q*) with anterior triangular part bearing articulation for lower jaw at inferior corner; a broad curved blade produced backwards from posterior edge and applied to inner face of preoperculum.

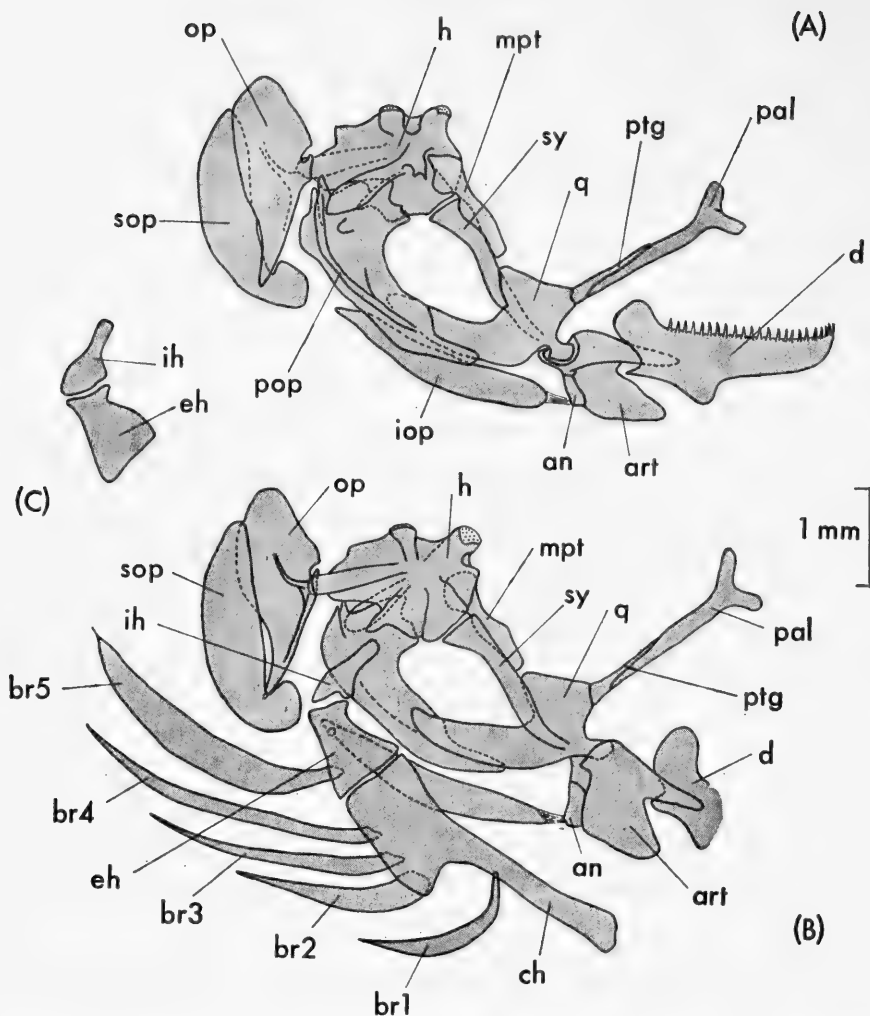


FIG. 10. Suspensorium of *L. orca*. (A) Lateral, (B) Median views. (C) Interhyal and epihyal bones, median aspect. Abbreviations as in text.

Preoperculum (*pop*) an integral part of suspensorium with strongly ridged posterior edge; upper part of wide anterior lamina firmly united with hyomandibular over wide area. Between preoperculum, symplectic, and quadrate exists a wide oval non-osseous foramen.

(ii) Palatopterygoid arch. Consists of two bones, pterygoid (*ptg*) a posterior splint applied to upper anterior corner of quadrate and lying along lower part of palatine, and palatine (*pal*) larger, anterior end with two heads, posterior head (*ppal*) articulating with ethmoid region, anterior (*apal*) with posterior face of proximal end of maxilla.

(iii) Upper jaw. Maxilla (*mx*) bearing outer ridge; distal end blunt with rounded

posterior margin ; proximal end with anterior lamina below posterior extension of premaxilla, and accommodating behind the anterior head of palatine. Premaxilla (*pmx*) pointed distally ; at proximal end, posterior tongue overlies process of maxilla ; medially, a long laterally compressed rod ascends over mesethmoid and together with fellow is embedded in oval plate of cartilage (not illustrated) related to mesethmoid groove. Premaxilla toothed along entire anterior edge.

(iv) Lower jaw. Articular (*art*) with large ventral plate. Angular (*an*) small, at posterior corner of articular. Dentary (*d*) toothed along upper edge anterior to relatively small blunt coronoid process.

(v) Hyoid arch. Consists of relatively large interhyal (*ih*), broad epihyal (*eh*), and large ceratohyal (*ch*) abruptly narrowing halfway along its length. Hypohyal (*hh*)

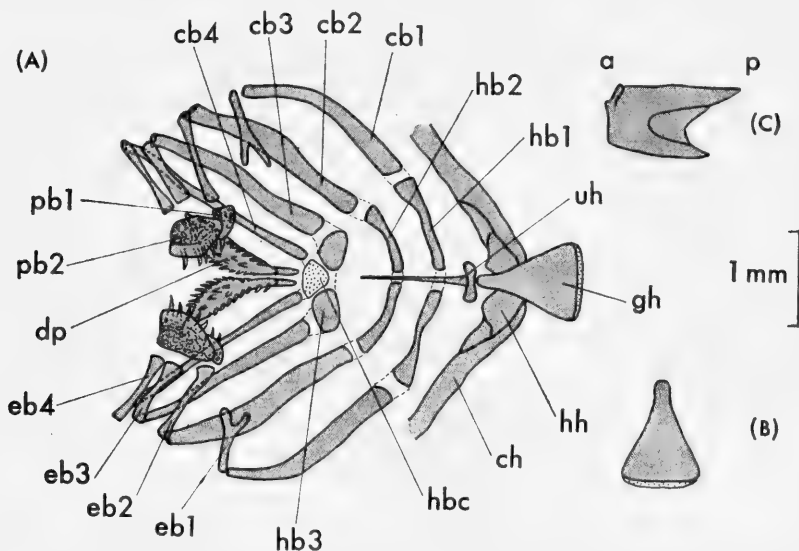


FIG. 11. *L. orca* : (A) Branchial skeleton, dorsal view. (B) Glossohyal, dorsal view. (C) Urohyal, lateral view. a, anterior ; p, posterior. Other abbreviations as in text.

firmly applied to anterior end of ceratohyal. Glossohyal (*gh*) fan shaped with straight anterior edge (Text-fig. IIB). Urohyal (*uh*) a vertical lamina with strongly emarginate posterior edge (Text-fig. IIC).

(vi) Branchial arches. Pharyngobranchials (*pb* 1, 2) represented by two dentigerous plates, the more posterior much larger and overlapping anterior one, opposite medial end of last three epibranchials. Epibranchials (*eb*) four, first one forked. Ceratobranchials (*cb*) four. Ventrally, first two hypobranchials (*hb* 1, 2) distinct ; a small round ossification (*hb* 3) in position of third, and a median cartilaginous plate (*hbc*) related to lower ends of fourth ceratobranchials. Fifth branchial arch represented by ventrolateral subtriangular dentigerous plate (*dp*) approaching fellow but separated in ventral midline. Ossified basibranchials absent.

(vii) Opercular series. Operculum (*op*) and suboperculum (*sop*) somewhat vertically elongate. Interoperculum (*iop*) long, anteriorly connected to angular by strong

ligament, posteriorly to outer face of epihyal near articulation of latter with interhyal. Branchiostegous rays (*bv* 1-5) five, uppermost and broadest attached to epihyal, next three to broad part of ceratohyal, and lowest and shortest to narrow section of ceratohyal.

(c) Pectoral Girdle (Text-fig. 12A). Cleithrum (*cl*) large, slightly bifid at upper end, in contact with fellow in ventral midline; at level of hypocoracoid, broad triangular process (Text-fig. 12B, *ctp*) meets pelvic element. Cleithrum joined by small supra-cleithrum (*scl*) to posttemporal (*pt*), which has two well developed anterior arms, with upper, stronger, to epiotic (*pts*), and lower, more slender, to exoccipital (*pti*). No hypercoracoid. Hypocoracoid (*hc*) small, at lower end of vertical part of cleithrum.

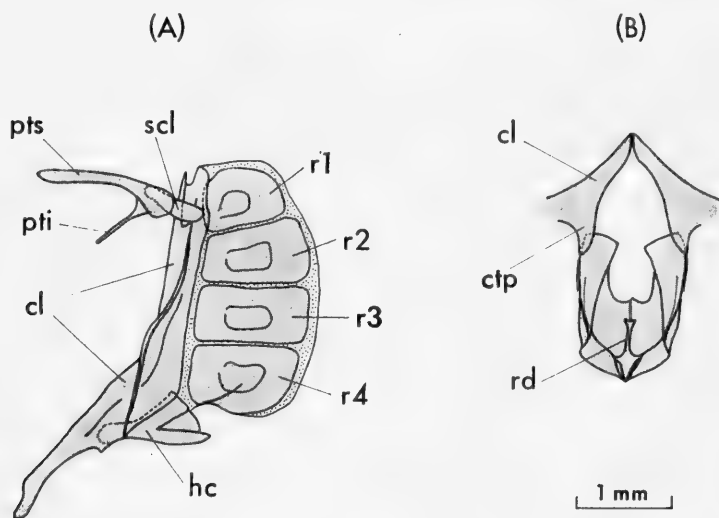


FIG. 12. *L. orca*: (A) Pectoral girdle, lateral view. (B) Pelvic girdle, ventral view. Abbreviations as in text.

Radials (*r* 1-4) large plates set in cartilage lamina attached along median side of posterior edge of cleithrum, with lower corner of most inferior radial joined by cartilage to upper part of posterior edge of hypocoracoid.

(d) Pelvic girdle (Text-fig. 12B). Each innominate bone consists of stout lateral section curving medially to form with fellow the posterior lip of girdle on which pelvic rays articulate except at median blunt protuberance, and a wide lamina arching dorsally and medially to join that from opposite side along median longitudinal suture. At posterior apex of girdle, a rod of bone (*rd*) with expanded base projects forwards ventral to lamina. Broad anterior ends of innominate bone related along lateral edge to median face of triangular process (*ctp*) from cleithrum (*cl*) of pectoral girdle.

(e) Axial skeleton. Vertebrae usually 27 (excluding urostyle); first five centra progressively shorter towards occiput, with first two shorter than wide. Third to thirteenth inclusive carry pleural ribs; twelfth to last complete vertebra with closed

haemal arches; first sixteen bear epipleurals. Last two epipleurals only ossified distally; in preceding two, ossified in two parts.

(f) Caudal skeleton (Text-fig. 13). Two large hypurals (*hyp*), upper fused to urostyle; along upper and lower edges of hypural fan lie splintlike epaxial (*epr*) and hypaxial (*hyr*) caudal radials. Lying freely between upper hypural and expanded neural arch of last vertebra occurs large roughly triangular epural plate (*epu*). Ventrally this may bear vestige of neural arch (*vna*), another part of which (*vnb*) occurs on anterior half of urostyle (*ur*). Neural (*nsp*) and haemal spines (*hsp*) of last three or four vertebrae are progressively expanded towards urostyle; on fusion of neural arch with postzygapophysis, root of arch comes to lie along whole length of centrum. Similar spread of haemal arches. Minor abnormalities found in caudal skeleton

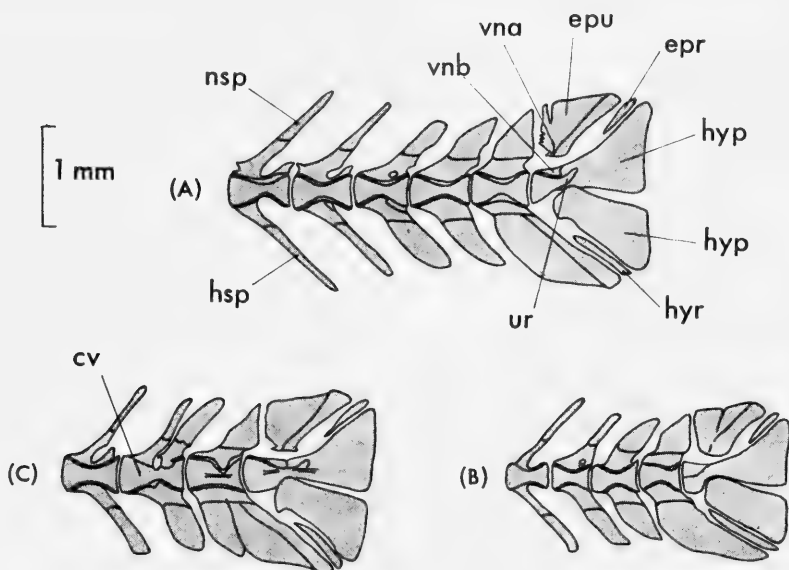


FIG. 13. Caudal skeleton of *L. orca*. (A) Normal. (B) Without vestigial neural arch. (c) With complex vertebra. Abbreviations as in text.

include loss of vestigial neural arch (*vna*, *vnb*), and a complex vertebra (*cv*), shown in Text-figs. 13B, C.

BIOLOGY

GEOGRAPHICAL DISTRIBUTION (Text-fig. 14). The genus *Lebetus* seems to be restricted to the European Atlantic boreal region, as defined by Ekman (1953). Outside the broad limits of this area, there are a few records of larval fishes from the Straits of Gibraltar, doubtfully assigned to *Gobius scorpioides* by Fage (1918). As yet, only young stages are recorded from southwest Iceland and the Faeroes; mature individuals no doubt remain to be discovered by systematic dredging in these waters. *Lebetus* does not appear to extend from the Belt Sea into the Baltic, and is also unknown from the southern North Sea and the eastern Channel. In the British

fauna, this goby was first known from a single example (BMNH 88. 3.22.9-10 part) obtained in Kilbrennan Sound and erroneously believed by Günther (1888) to represent the mature male of his *Gobius jeffreysii*. Collett (1896) drew attention to this mistake, and in 1898 Holt & Byrne recorded a ripe female (as *G. scorpioides*) from Falmouth Harbour. A full list of records covering the entire area of distribution is provided in the Appendix.

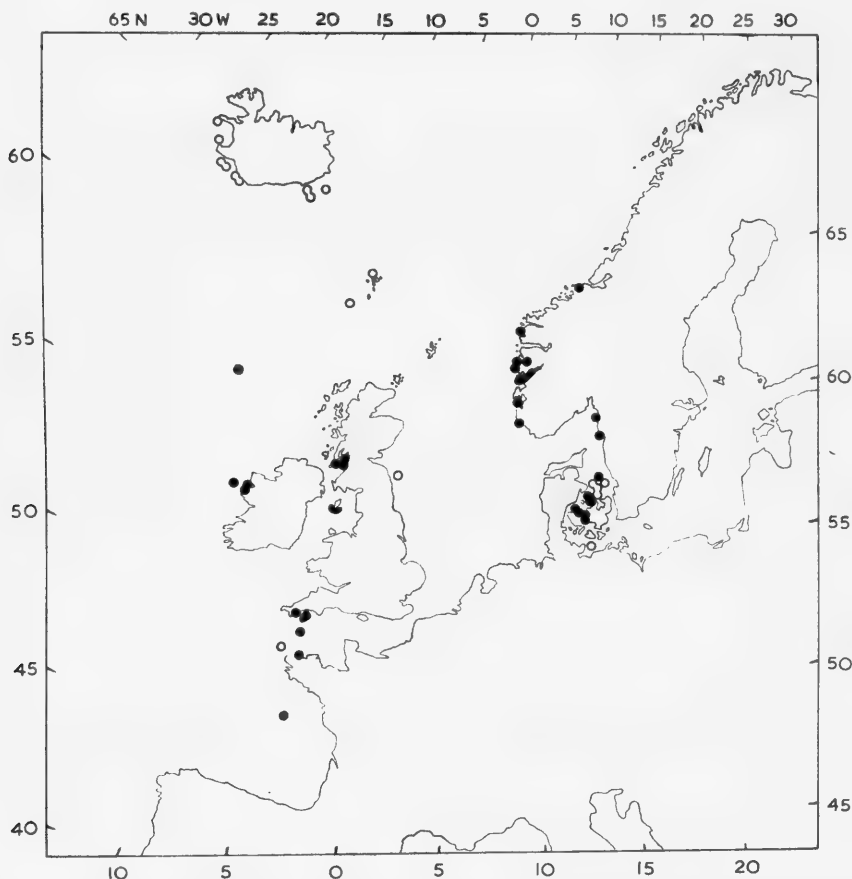


FIG. 14. Geographical distribution of *L. orca*. Locality and not number of records is indicated. Open circles denote localities from which there are only records specified as planktonic.

ECOLOGICAL DISTRIBUTION. *Lebetus orca* has been taken over a wide bathymetric range, from about 2 m. (Holt & Byrne, 1903) to 375 m. (Lilljeborg, 1884; Collett, 1902), chiefly from coarse grounds but also on mud (Patience, 1906). Le Danois (1913) regarded *Gobius scorpioides guilleoti* as a characteristic inhabitant of the "maerl" deposits of calcareous algae (*Lithothamnion* spp, *Lithophyllum*) in the bays and estuaries near Roscoff although, to judge from the listed fauna and flora, these estuaries could hardly have shown a marked reduction in salinity. This type of

bottom was classified by Le Danois among the sandy and muddy sand areas of the "littoral" zone, extending down to 40 m. Together with representative animals, including *Lebetus*, a stretch of maerl is imaginatively depicted in water-colours by Le Danois (1953).

In Manx waters (Text-fig. 15), where the bottom fauna and deposits have been reviewed by Jones (1951) and Southward (1957), the species has been found on grounds ranging from muddy sand to stones and coarse gravel, always with dead shells. Calcareous algae (e.g. *Lithothamnion*) are common on stones in this area; near the shore, larger weeds may be present, and other localities where *Lebetus* has been collected are notable for the abundance of the polyzoan *Flustra*, various

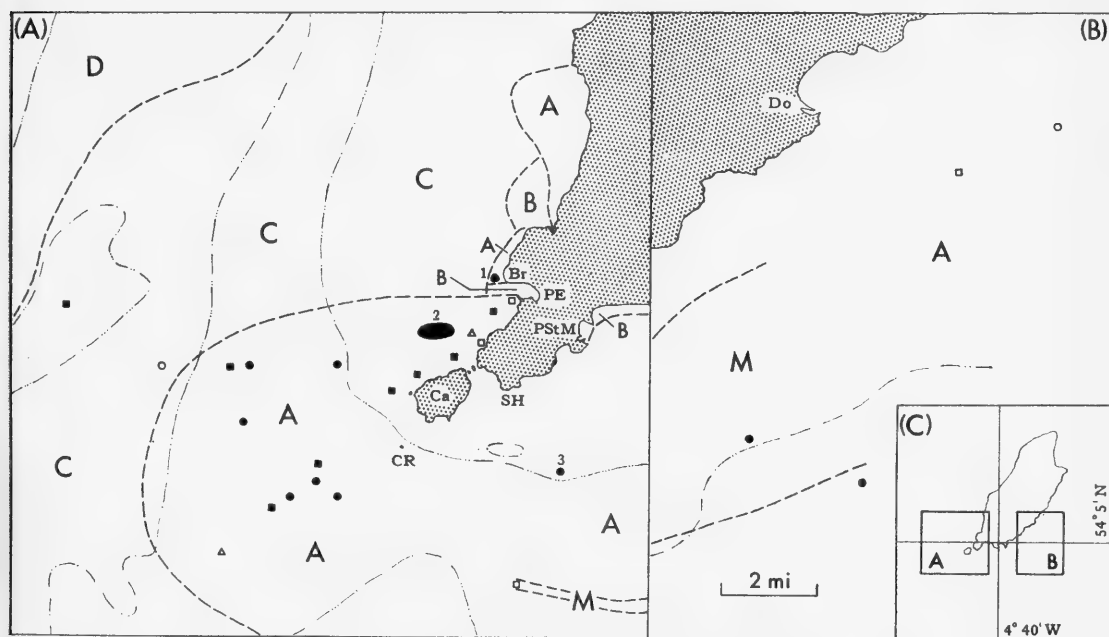


FIG. 15. Distribution of *L. orca* off the southern end of the Isle of Man. Position of areas A and B shown in C. Symbols indicate number of individuals in *orca* and *scorpioides* coloration groups respectively thus: ■, 1 *orca*; □, 1, and △, 2 *scorpioides*; ○, 1 *orca* and 1 *scorpioides*; station 1, 2 *orca* and 3 *scorpioides*; station 2, 10 and 11; station 3, 4 and 3; ●, records by Jones (1950) not examined by the author. A, stones, gravel, shell; B, fine sand; C, muddy sand; D, mud; M, *Modiolus* epifauna; - - -, approximate limits of the various deposits; - . . . -, 20 fm. (36.6 m.); - . . . -, 30 fm. (54.9 m.); - . . . -, 40 fm. (73.2 m.). Scale in nautical miles. Br, Bradda Head; Ca, Calf Island; CR, Chicken Rock; Do, Douglas; PE, Port Erin; PStM, Port St. Mary; SH, Spanish Head.

ophiuroids, or the lamellibranch *Modiolus modiolus* (L.). Off the Isle of Man, *Lebetus* has been found at depths from 18 to 51 m.; trawling in shallower water over the sandy bottom of Port Erin Bay and runner-dredging in deeper water on mud and finer muddy sand to the west of the island have both failed to reveal the occurrence of this species, even when the collecting gear included a bag of fine-meshed material.

Le Danois (1913) suggested that the rosy or violet coloration of *Lebetus* was a cryptic adaptation to a background of *Lithothamnion*, but the species has been obtained in the Manx area from localities where calcareous algae are missing from the dredge haul. In general, *Lebetus* is probably common on the coarser grounds around the southern end of the Isle of Man and may extend on to softer deposits where ample cover in the form of dead shells is available. Other small teleosts obtained in the same area include the rockling *Ciliata septentrionalis* (Collett), the dragonets *Callionymus maculatus* Rafinesque and *C. reticulatus* C. & V., the blennioids *Blennius ocellaris* L., *Pholis gunnellus* (L.) and *Chirolophis ascanii* Walbaum, the gobies *Buenia jeffreysii* (Günther) and *Pomatoschistus pictus* (Malm), the cottid *Acanthocottus lilljeborgi* (Collett), and the clingfish *Diplecogaster bimaculata* (Bonnaterre).

DIET. A total of 48 guts were examined, all from the Manx region. Nine of these were completely empty, and a further eight contained only a trace of food. The method adopted in assessing diet was a modification of the points system described by Hynes (1950). The number of points awarded to a stomach depended on fullness, 20 being scored by a full stomach, and this was then divided between the food items present in relation to their volume as estimated by eye. A proportionate number of additional points was allotted to food in the remainder of the gut. Half points were awarded to items occurring in very small quantities; in practice this convention enables the more insignificant items to be considered with the rest and does not result in any obvious artificial exaggeration of the importance of these constituents. Results are shown in Table IX.

Rather more than half of the gut contents was made up of crustacea. Three species of decapods together comprised the most important part of this; amphipods, chiefly Gammaridea, formed another major component but only *Amphilocheus manudens* Bate was identified among this group. None of the ostracods or harpacticoid copepods were named although these comprised an appreciable fraction of the diet. Polychaetes and lamellibranchs were the other notable food items. The vast majority of polychaete material consisted of the polynoid *Harmathoe*, which was by far the most abundant animal of any group identified in the food. About half the lamellibranch remains were unidentifiable; in the rest, the occurrence of an intact example of *Musculus marmoratus* (Forbes), 2.5 mm. long, in a fish of only 25 mm. may be noted. These findings suggest that *Lebetus*, like many other gobies, is exclusively predatory, feeding on small demersal animals. The species named are all typical of the coarser grounds inhabited by *Lebetus*. The presence of a serpulid stalk and cirripede thoracic limbs in two guts indicates that rather larger animals may be attacked, probably when the goby is attracted by movement of some appendage.

ENDOPARASITES. The parasites recorded in Table X were found during removal and inspection of guts from the Manx specimens of *Lebetus*. None appears to be common. Ectoparasites were not seen on any of the fishes studied.

REPRODUCTION. (a) Reproductive organs. The male genitalia of *Lebetus* (Text-fig. 16) display several peculiar features. The mature testes are relatively small, oval to moderately elongate, somewhat flattened bodies lying against the roof of the abdominal cavity, up to 1.5 mm. long by 0.19–0.38 mm. wide. Each testis has about 20–30 transverse lobules, enclosed by a definite tunic and emptying into a median

TABLE IX.—*Gut Contents, Number of Points Awarded, and Percentages of Total Points Awarded to Identifiable Gut Contents for More Important Constituents*

	No. of points	% of total points awarded to identifiable gut contents
POLYCHAETA		
<i>Harmathoe</i> sp. (<i>impar</i> ?)	58	25.3
<i>Pholoë minuta</i> (Fabr.)	7	
Phyllodocid indet.		
Serpulid opercle and stalk		
total	1	
CRUSTACEA		
Crustacean debris	13½	55.4
Ostracods	21	8.1
Harpacticoid Copepods	11½	4.4
Amphipods indet.	32½	15.0
<i>Amphilocheus manudens</i> Bate	1½	
<i>Paratanais batei</i> G. O. Sars	2	
Cirripede appendage	½	
Caprellid indet.	5	
Decapod appendages	1	
Hippolytid (<i>Spirontocaris</i> ?)	39	21.8
<i>Galathea</i> sp.	4	
<i>Pagurus bernhardus</i> (L.)	13	
PYCNOGONIDA		
<i>Ammothea</i> sp.	2	
<i>Pallene</i> sp.	1	
MOLLUSCA		
Shell fragments	1½	12.6
Gastropods indet.	5	
Lamellibranch indet.	17	
<i>Musculus marmoratus</i> (Forbes)	3½	
<i>Chlamys</i> sp., newly settled	½	
<i>Hiatella arctica</i> (L.)	12	
ECHINODERMATA		
Ophiuroid indet.	7	
SAND GRAINS	1	
UNIDENTIFIABLE MATERIAL	49½	

TABLE X.—*Endoparasites Recorded from 48 Manx Examples of Lebetus orca*

Parasite	No. of fishes infected	Site of infection
TREMATODA DIGENEA		
<i>Plagioporus</i> sp.	5	intestine (3), rectum (2)
<i>Derogenes</i> sp., unencysted metacercaria	1	stomach
CESTODA PSEUDOPHYLLIDEA		
<i>Bothriocephalus</i> larvae	2	intestine (1), rectum (1)
NEMATODA ASCAROIDEA		
Anisakid larvae	3	abdominal cavity

longitudinal sperm duct. There is no pronounced band of the so-called interstitial tissue which occurs in the testes of some other gobiids (Eggert, 1931; Vivien, 1939; Coujard, 1941). Posterior to the testes, each sperm duct pursues a long and independent course to the seminal vesicle of that side. This condition appears to be derived from one in which the testis was longer with spermatogenic lobules along the entire length of the duct, since vestigial lobules are sometimes visible on the free duct in immature fishes (Text-fig. 16D). The seminal vesicles, small in the immature male (Text-fig. 16C), increase greatly in size with maturation, the anterior tips in some cases reaching as far forward as the posterior ends of the testes. They are transparent in life, conspicuously lobulate, without specialized regions, and empty into the united sperm ducts, which also receive the secretion from a small accessory glandular mass

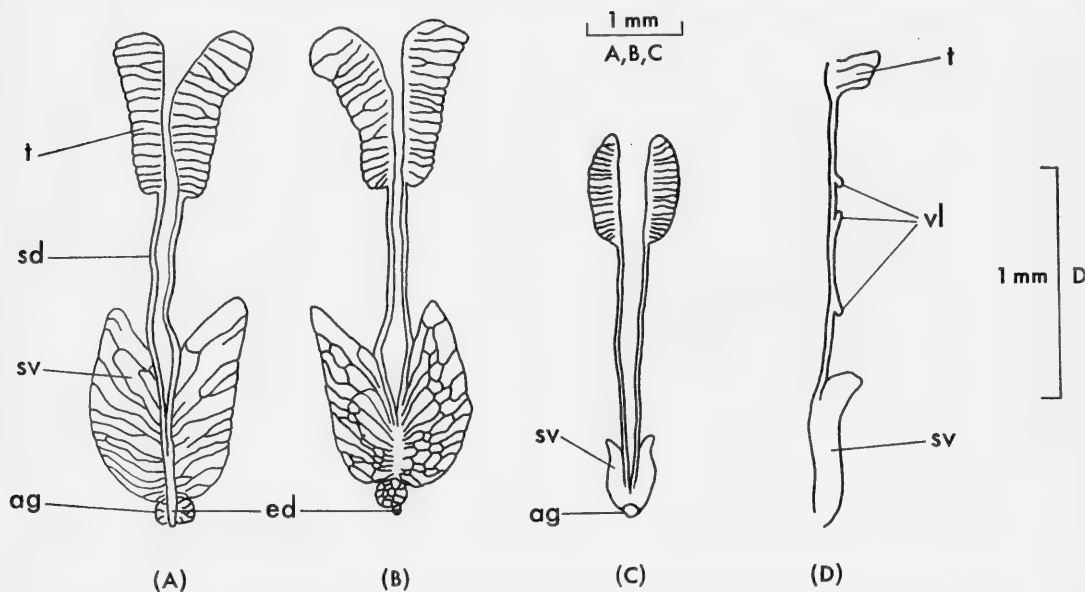


FIG. 16. Male genitalia of *L. orca*. Mature (A) dorsal view, (B) ventral view, and (C) immature, ventral view. (D) Sperm duct with vestigial lobules in immature fish. t, testis; sd, sperm duct; sv, seminal vesicle; ag, accessory gland; ed, ejaculatory duct; vl., vestigial lobules.

at the posterior ends of the seminal vesicles. The urogenital papilla of the mature male (Text-fig. 17A) terminates in a circlet of long vascularized processes. During fertilization these may perhaps embrace the tip of the egg and achieve an economy of sperm correlated with the small size of the testes. The surface of the male urogenital papilla carries a scattering of melanophores in adult specimens. In the female, the ovaries present the usual cystovarian appearance and are paired. Ripe oocytes reach a maximum diameter of probably about 0.6 mm. (Holt & Byrne, 1898; personal observation). The urogenital papilla (Text-fig. 17B) is stouter than that of the male, with the terminal villose processes shorter and broader, and, as in the immature male (Text-fig. 17C), lacks surface pigmentation.

(b) Breeding season. Holt & Byrne (1898) recorded a ripe female from Falmouth Harbour in mid-July, and, in the nearby Plymouth area, Russell (1930b-1940) found postlarval *Lebetus* from May to October and also in December, with August as the month of greatest abundance. Bal (1940a, b) obtained postlarvae in late June and July off Port Erin, Isle of Man. At Roscoff, Cantacuzene (1956) stated that the spawning season was from April to September. In the Manx material, females with swollen ovaries containing opaque yellow oocytes were present from mid-February to mid-June. Because of reduction in the amount of dredging performed, only one specimen—a male—was obtained in July and none at all in August. In early September a female was taken with ovaries showing possible traces of oocyte resorption, a process characterizing the termination of the breeding season in other gobies (Prasad, 1959 ;

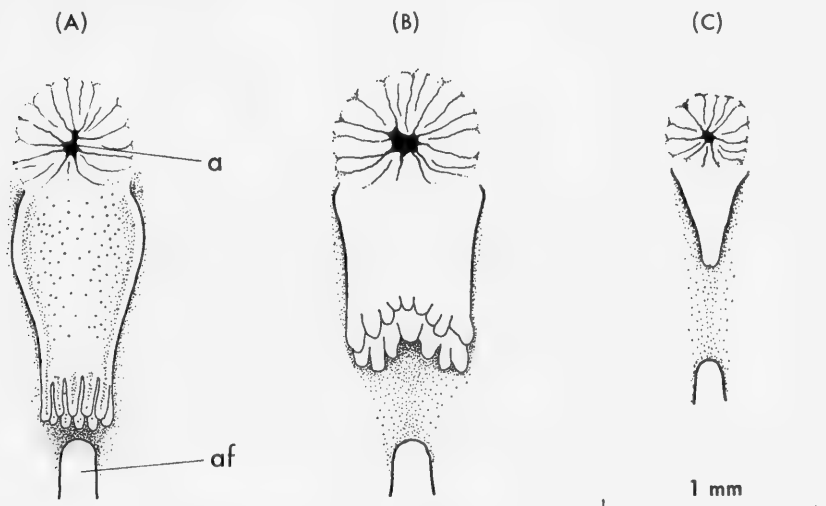


FIG. 17. Urogenital papillae of *L. orca*. (A) Mature male. (B) Mature female. (C) Immature male. a, anus ; af, origin of anal fin.

Miller, 1961a). Fully mature males were obtained from February to July. In all probability the breeding season commences in March and may extend to August. Within such a period it seems possible that a number of broods may be produced by one female, but attempts to investigate this from size frequency distribution of oocytes have been unsuccessful because of failure to obtain a fully ripe ovary. The fertilized egg and early developmental stages of this species are unknown.

(c) Fecundity. The ovaries of four females of standard lengths 24.0, 25.0, 25.5, and 28.0 mm. contained respectively 185, 140, 270, and 194 ripening oocytes. The relatively low number of these is in accordance with the small size of this goby and are comparable to values made available by Dôtu for some small Japanese species. Thus individuals of *Paleatogobius uchidae* Takagi, 23 to 38 mm. in standard length, possessed 158-430 "ovarian eggs", *Luciogobius saikaiensis* Dôtu, 25-32 mm., 66-148, and *Eutaeniichthys gilli* Jordan & Snyder, 35-40 mm., 86-310 (Dôtu, 1955, 1957a ; Dôtu & Mito, 1958). In *Gobiosoma robustum* Ginsburg from Tampa Bay, Florida, Springer

& McErlean (1961) recorded 56-462 'large eggs' in females from 15-28 mm. However, larger numbers were found in *Acentrogobius masago* (Tomiya) (14-26 mm., 264-961) and *Tridentiger undicervicus* Tomiya (24-38 mm., 1,812-5,770), while *Gobius lidwilli* McCulloch, a species smaller than *L. orca*, contained from 154-311 eggs at 15-16 mm. (Dôtu, 1957*b*, 1958*a,b*). In the Philippine *Mistichthys luzonensis* Smith, where adult females attain lengths of 11-14.5 mm., Te Winkel (1935) counted only 20-40 mature ova per fish.

(*d*) Sexual dimorphism. This is expressed in coloration, and size of the dorsal and anal fins. There appears to be no divergence in body proportions between the sexes

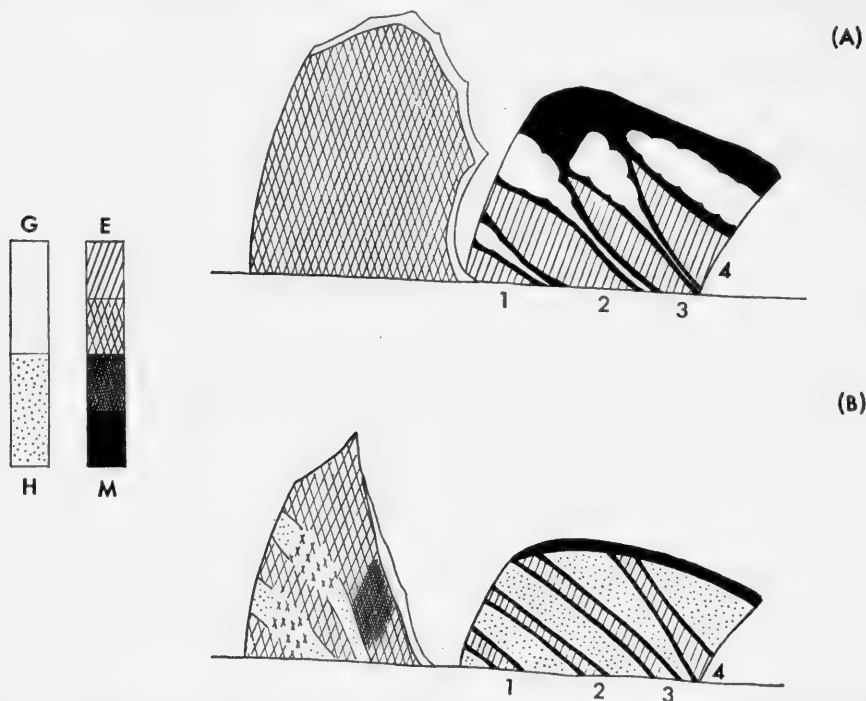


FIG. 18. Homologous areas in coloration of dorsal fins in mature male (A) and female (B) of *L. orca*. H, hyaline fin membrane; G, guanophores; E, erythrophores; M, melanophores; 1-4, comparable bands of erythrophores in second dorsal fin. Increasing admixture of melanophores with erythrophores shown by closer cross-hatching.

and both reach about the same maximum standard length. Detailed accounts of the coloration of mature individuals in each sex have been given above. Differences are most pronounced in the two dorsal fins, but pelvic, pectoral, and anal fins are all darker in the male than in the female. The components of the dorsal fin patterns are basically the same in the two sexes, and the considerable disparity between adult males and females results more from differential emphasis and spread of existing parts than from the appearance of new elements as maturity is approached. Homologous parts of the dorsal fin coloration are shown diagrammatically in Text-fig. 18. On reaching the size of maturity, dimorphism in fin size is brought about by

changes in the growth of individual rays and adjacent membrane (Text-figs. 19, 20). Growth of the second ray (II) of the first dorsal fin is about the same in the two sexes, but differences in length become more apparent in the other first and second dorsal rays investigated, especially the posterior ones of the first dorsal fin, these rays attaining a greater length in males than in females. In the male, the first dorsal membranes have considerable elasticity, and an enormous spread is achieved at full extension of the fin (Pl. I). Growth of the anal fin was not studied in detail, but a divergence in size at sexual maturity is indicated in the systematic description above.

Sexual dimorphism in teleosts has recently been reviewed by Bertin (1958). The phenomenon is of widespread occurrence among the gobies and has been investigated in Japanese species by Egami (1960). This worker lists a number of species in which the first dorsal rays are more elongate in the male, but does not mention any instances of sexual differences in coloration of the dorsal fins. In searching for dimorphism in ray length, Egami compares the lengths of only the longest ray in each fin. With the first dorsal fin of *Lebetus*, where such dimorphism in fin size is most conspicuous, this method of comparison is inapplicable since the longest ray in this fin reaches a similar length in both sexes and by itself would fail to indicate the great disparity between male and female in growth of the shorter first dorsal rays. The secondary sexual characters in *Lebetus* are probably involved in the release of certain sequences in reproductive behaviour. The enlarged dorsal fins of the male, with the contrast of bright colours disposed in an arrangement peculiar to the species, have all the characters of sign stimuli. Spawning activities in several European gobiids, where sexual dimorphism in coloration and shape of the dorsal fins may occur, are known to involve display of these fins by the male in fighting and courtship (Kinzer, 1960).

LIFE HISTORY AND GROWTH. Scale readings from Manx *Lebetus* have been interpreted in the light of unpublished data concerning scale growth in the goby *Pomatoschistus microps* (Krøyer). Results indicate that *Lebetus* may live for at least two years. In some individuals, sexual maturity may be attained at the age of about one year, while in others this stage is not reached until after the second winter of life. Insufficient material exists for studies on growth rate; the largest specimen collected, a male, was 30.0 mm. in standard length (total 37.5 mm.) and in the second autumn of life. The largest female, 29.0 + 7.0 mm., was probably nearing the end of its second year. The maximum size recorded for the genus is 39.0 mm. (Lönnerberg & Gustafson, 1935). Among the Manx collection, the smallest mature male and female individuals were 22.0 and 23.75 mm. in standard length, but Holt & Byrne (1898) obtained a ripe female of only 21.0 mm. total length. Further investigation of the life history of this species must depend on a more satisfactory means of sampling, since the scallop dredge, even when lined with fine meshed netting, appears to be highly selective of older and larger fishes.

DISCUSSION

The percomorph suborder Gobioidae was defined in osteological terms by Regan (1911). Since then, the skeletons of individual species have been treated by Gregory (1933), Te Winkel (1935), Lele & Kulkarni (1938, 1939), Petit (1941), Smith (1951), and Matsubara & Iwai (1959), while Gosline (1955) has recently compared those of

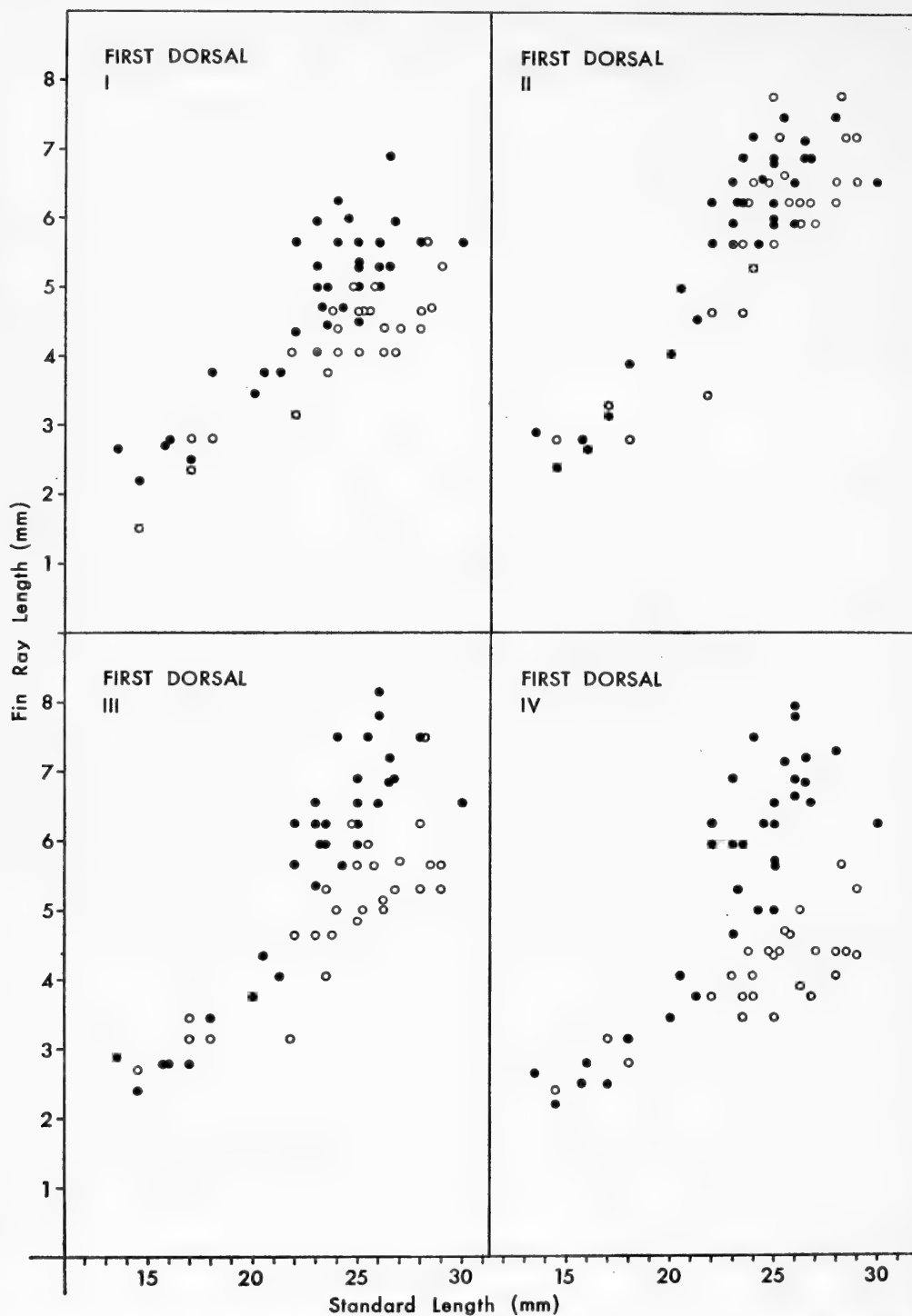


FIG. 19. Relation between standard length and lengths of first four rays of first dorsal fin (I-IV) in *L. orca*. ●, male; ○, female; ⊙, coincident points.

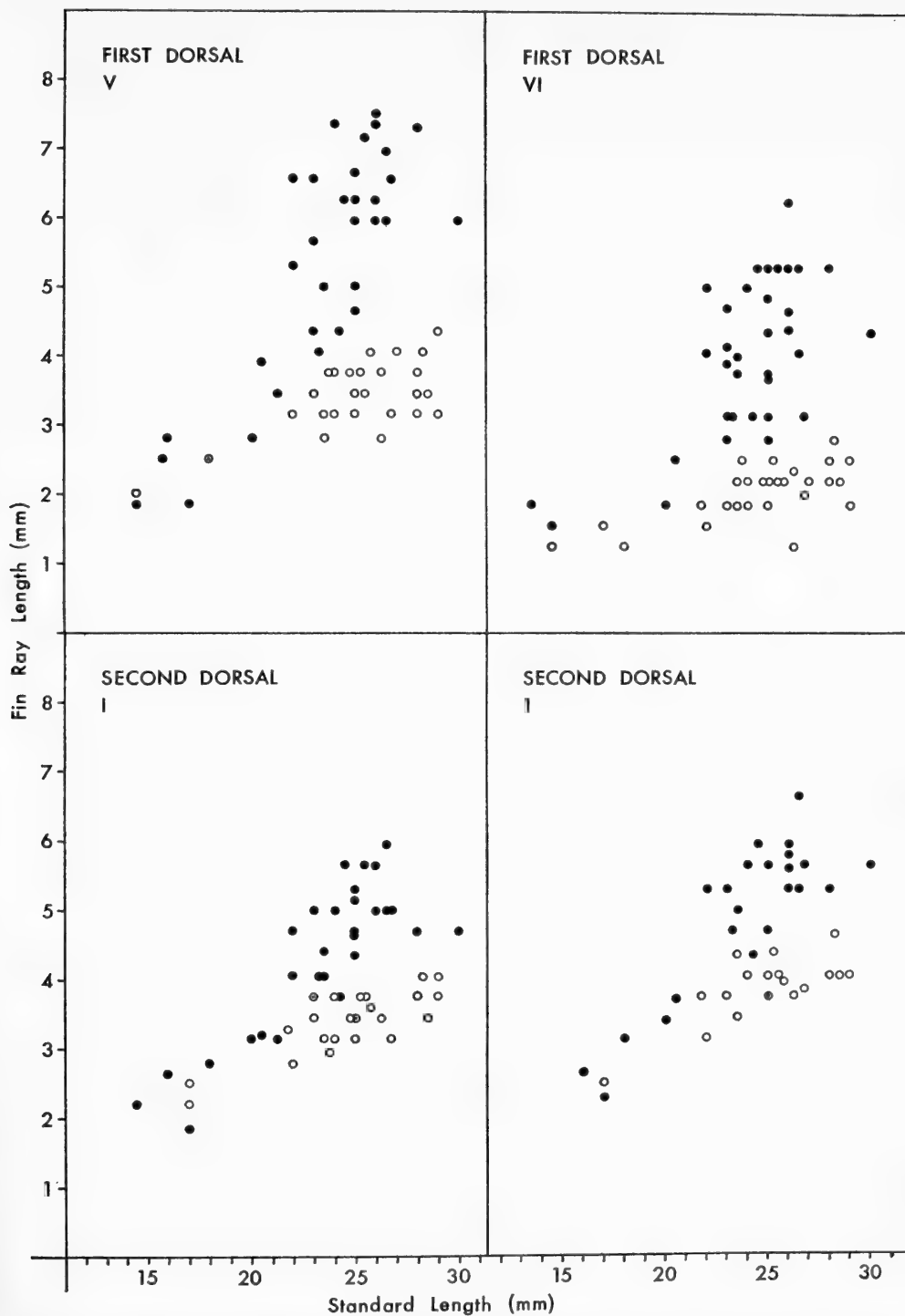


FIG. 20. Relation between standard length and length of last two rays of first dorsal fin (V, VI) and first two rays of second dorsal fin (I, I) in *L. orca*. Symbols as in Fig. 19.

eight diverse genera of gobies. The group is characterized by several peculiarities. Among these are the large non-osseous area between the symplectic, quadrate, and preoperculum; the arrangement of the branchiostegals on the ceratohyal; the absence of the parietal bones; and the presence of a splintlike radial above and below the hypurals in the caudal skeleton. In all these features, the genus *Lebetus* appears as a typical gobioid fish, but there has been some doubt about the position of *Lebetus* among the families of this suborder. Of these about six are now recognized (Koumans, 1953; Gosline, 1955; Norman, MS.). The Rhyacichthyidae, Taenioididae, Kraemeriidae, and Microdesmidae are highly aberrant gobioids and need not be further dealt with in this discussion. The two largest and most important families are the Eleotridae and Gobiidae. Skeletal differences between these have been summarized by Regan (1911), and the diagnostic value of certain features reviewed by Gosline (1955). Nevertheless, in referring gobies to one or other of these families, it has been customary to use the external form of the pelvic fins as the chief guide in the usual absence of osteological data. According to Regan (1911) and other authors, the Eleotridae are characterized by the pelvic fins being separate, and the Gobiidae, when these fins are developed, by their union to produce a simple cup-shaped disc. However, various stages in the union or separation of the pelvic fins have been recognized among gobioid genera and the importance of this feature as a criterion of family position has recently been questioned, especially by Böhlke & Robins (1960a, b) who have found eleotrid, gobiid, and intermediate types of pelvic fins in a single genus (*Coryphopterus* Gill). In such cases as these, determination of systematic position within the suborder requires investigation of the skeleton.

When erecting the genus *Lebetus*, Winther (1877) emphasized that the anterior membrane of the pelvic disc was missing, although the two fins were joined along their entire length in the midline. At first accepting (1885) the new genus, Collett (1896) was later of the opinion that intermediate stages in reduction of the anterior membrane could be found between the fully developed condition in *Gobius* and complete loss as reported for *Lebetus*, and doubted the validity of separating the latter from *Gobius*. On the other hand, Duncker (1928) found that the two pelvic fins were completely separated in *Lebetus* but stressed the desirability for re-examination of these fins in better preserved material in order to decide whether *Lebetus* belonged to the Eleotridae or the Gobiidae. De Buen (1930b) associated *Lebetus* with two Mediterranean genera, one of which had previously been regarded as an eleotrid because of its almost completely separated pelvic fins, and placed this "*Lebetus*" group in the subfamily Gobiinae of the Gobiidae. Koumans (1931) similarly accepted *Lebetus* as a gobiid genus. In the present work, it has been confirmed that, in the least damaged examples, the pelvic fins of *Lebetus* are completely united between their origins and the distal extremity of the fifth ray of each fin, but are entirely without trace of an anterior membrane to complete the disc. To settle the question of family position with greater certainty, it became obvious that examination of the skeleton was necessary, and the results of this study reveal that *Lebetus* has the characters of a typical member of the Gobiidae. These include a T-shaped head to the palatine, loss of the mesopterygoid from the palatopterygoid arch, and absence of a hypercoracoid in the pectoral girdle, where the laminar radials are inserted on the cleithrum

and the lowest also related to the hypocoracoid. In the possession of a spatulate glossohyal, five branchiostegous rays, a reduced metapterygoid, and loss of the opisthotic, *Lebetus* also reaches a higher level of specialization than that described among the eleotrids (Regan, 1911; Takagi, 1950; Gosline, 1955).

Within the Gobiidae, the affinities of *Lebetus* undoubtedly lie with the subfamily Gobiinae, since the genus exhibits none of the more extreme modifications of the Sicydinae, Periophthalminae, Apocrypteinae, Tridentigerinae, Gobiodontinae, or Benthophilinae (Koumans, 1953; Norman, MS.). In the absence of an anterior membrane to the pelvic disc, *Lebetus* resembles a number of small Indo-Pacific genera i.e. *Herreogobius* Koumans, *Quisquilius* Jordan & Everman, *Fusigobius* Whitley, *Amblyogobius* Bleeker, and *Zonogobius* Bleeker (Koumans, 1953; Gosline, 1959). With head and anterior part of body naked, elongate rays in the first dorsal fin, 22–30 scales in lateral series, and radial formula of D_2 1/8–9, A 1/7–8 (Koumans, 1953), *Zonogobius* appears to be closest of these to *Lebetus*. Differences comprise the larger gill openings, and more laterally compressed head in *Zonogobius*. However, it is impossible to trace relationships between European and exotic genera, when the arrangement of the lateral line system in so many of the latter, including *Zonogobius*, remains to be adequately described and figured. As shown in the normal illustration of *Zonogobius corallinus* sp. nov. (Mozambique) by Smith (1959, Fig. 29), the distribution of sensory papillae on cheek and postorbital regions differs from that of *Lebetus* in the complete longitudinal rows and more numerous papillae. Koumans (1931) associated *Lebetus* with the genus *Coryphopterus* Gill; as defined by Koumans, the latter included European *Pomatoschistus* species together with the genotype, *C. glaucofraenum* Gill, from the tropical Western Atlantic. In a revision of *Coryphopterus* sensu stricto, Böhlke & Robins (1960b) provide details of the cephalic lateral line system and other characters which do not point to any close affinity with *Lebetus*, in spite of the fact that two of their new Western Atlantic species (*C. alloides* and *C. dicrus*) are without the anterior pelvic membrane.

In the European fauna there are two Mediterranean genera of gobies lacking anterior membranes to the pelvic fins. These are *Odondebuenia* and *Cabotia*, both introduced by De Buen (1930b). Since *Cabotia* is preoccupied among the Lepidoptera, De Buen (15th June, 1940) suggested *Fagea* as a replacement but was preceded in this by Whitley (May, 1940) who introduced *Cabotichthys*. The genus *Odondebuenia* contains two species which were originally (1907) placed among the Eleotridae as *Eleotris balearicus* Pellegrin & Fage and *E. pruvoti* Fage. *Odondebuenia* is characterized by pelvic fins united only at their bases, naked nape and throat, unusual gill rakers (Fage, 1907, figs. 3 and 9), modified scales at the origin of the caudal fin, and meristic characters of D_2 1/9–11, A 1/8–10, and Sc.1.1.24–32. Both species of *Odondebuenia* show sexual dimorphism in length of first dorsal fin rays (Fage, 1918; De Buen, 1930b). The second of these Mediterranean genera, *Cabotichthys*, has the pelvics joined together for about half their length, nape and throat fully scaled, scales of the caudal peduncle not modified, and fin ray and scale counts of D_2 1/14, A 1/13, and Sc. 1.1.50. The genus is founded on one species, *C. schmidtii* (De Buen) known only from the single type specimen (De Buen, 1930b). De Buen (1931) included *Odondebuenia*, *Cabotichthys* and *Lebetus* in his "*Lebetus*" group of genera, the principal

character of which is the absence of the anterior pelvic membrane. Similarities in habitat also link these fishes, all three being obtained on coarse grounds where calcareous algae are noticeable constituents of the bottom deposits, and none exceed 50 mm. in length.

On the face of the diagnoses given above, *Lebetus* would appear to be fairly closely related to *Odondebuena* except for the occurrence in the latter of modified caudal scales and gill rakers, and the greater separation of the pelvic fins, while *Cabotichthys* stands quite distant from both in several respects. The lateral line system in *Odondebuena* and *Cabotichthys* has fortunately been investigated by De Buen (1930b, 1940) and that of *Lebetus* is described above. Comparison of these accounts for the three genera reveals the heterogeneous nature of their grouping. The patterns of sensory papillae and extent of the cephalic canals in *Cabotichthys* point to an intimate connection with the genus *Gobius*, as defined by De Buen (1930a, 1931), and, apart from the reputed form of the pelvics, other characters of this fish do not warrant any generic separation from *Gobius*. My own experience with dredged and trawled examples of *Lebetus* and other gobies is that the pelvic membranes are very susceptible to damage, and the pelvics of *Cabotichthys*, as figured by De Buen (1930b, fig. 7) are reminiscent of such a condition. It may well prove that *C. schmidtii* is no more than a damaged specimen of a *Gobius* species.

The state of the pelvics in the *Odondebuena* species seems well established from a number of specimens. In the arrangement of sensory papillae, this genus differs markedly from *Lebetus* in the greater number of papillae, and their distribution in well marked transverse and longitudinal rows on the cheek approaches that in *Gobius*, which *Odondebuena* also resembles in the possession of a similar cephalic canal system. The morphological attributes common to both *Odondebuena* and *Lebetus* are not of a very highly specialized nature and do not outweigh the considerable disparity in patterns of sensory papillae. Modification of scales at the base of the caudal fin involves pronounced elongation of all the ctenii in *O. pruvoti* (Fage, 1907, fig. 7) or merely the lateral ctenii in *O. balearica* (Fage, 1907, fig. 11; De Buen, 1930b, fig. 2). Although not seen in *Lebetus*, it is of interest to note the occurrence of this peculiarity in the new gobioid genus *Varicus*, recently described from the West Indies by Robins & Böhlke (1961) and also with separated pelvic fins. These authors commented on the existence of comparable scales in the Californian eleotrid *Chriolepis* Gilbert and the gobiid *Garmannia* Jordan, which is represented on both sides of Central America and in the Caribbean. It is not proposed at this point to deal further with the relationships of *Odondebuena*, except to call attention to the need for an osteological investigation of this genus.

Loss of the anterior membrane from the pelvic disc has probably occurred on a number of different evolutionary lines among the Gobiidae and, as in the case of *Odondebuena* and *Lebetus*, need not be a sure indication of close phyletic association. In geographical distribution *Lebetus* appears to be confined to the eastern Atlantic boreal region and may well have evolved there. It is in this area, therefore, that the closest relatives of the genus may be sought. Eight other gobioid genera are recorded from the eastern North Atlantic (De Buen, 1931) and all of these have a pelvic disc complete with anterior membrane. The two pelagic forms *Aphyia* Risso and *Crystal-*

logobius Gill may be excluded from consideration on the grounds of extreme specialization. Among the demersal gobies, the genera *Deltentosteus* Gill, *Pomatoschistus* Gill, *Chaparrudo* De Buen, and *Gobius* L. exhibit various features of anatomy and lateral line organization (see De Buen, 1930a, 1931) which do not suggest any near relationship with *Lebetus*. The remaining genera, *Lesueurigobius* Whitley and *Buenia* Iljin, deserve more attention. The first of these, represented by *Lesueurigobius friesii* (Collett), has a number of characters in common with *Lebetus*. Thus both genera are entirely without cephalic canals and in disposition of sensory papillae show a posterior extension of row *a* behind the eye, papillae in the oculoscapular furrow (row *u*), interorbital papillae, a high posterior termination for row *i*, and reduction of rows *m*, *n*, and *o* (Sanzo, 1911, pl. 9, figs. 4, 5, as *Gobius macrolepis*; De Buen, 1923, figs. 21, 22). However, the great abundance of papillae in *Lesueurigobius* contrasts with their relative scarcity in *Lebetus*, where several rows (*g*, *x*, *z*, *c*², *b*, *d*) found in *Lesueurigobius* are little if at all developed, and others (*i*, *e*, *ot*, *c-cp*) interrupted. Except for reduction in rows *m*, *n*, and *o*, the resemblances listed may be accounted for by independent action of a similar evolutionary process in the past history of each genus. This was the replacement of existing cephalic canals by rows of sensory papillae. Considerable anatomical differences in size, habit, squamation, radial formulae, and coloration (Holt & Byrne, 1903; Duncker, 1928) would also suggest similarities are due to convergence, and that any affinity is relatively distant. No closer relationship can be demonstrated with *Lesueurigobius sanzoi* (De Buen) or *L. lesueuri* (Risso) from the Mediterranean (De Buen, 1923).

The only genus now remaining is *Buenia*, the Atlantic species of which is *B. jeffreysii* (Günther), and it is with this form that *Lebetus* appears at present to be most closely connected. Lacking scales on the head and predorsal regions, and with meristic characters of D₂ 1/8-9, A 1/7-8, and Sc. 1.1.25-30 (Duncker, 1928; personal observation), *B. jeffreysii* displays a resemblance to *Lebetus* which is also evident in the arrangement of the lateral line system (Text-fig. 21). On the cheek absence of transverse rows of papillae, and the short row of large papillae with an intermediate papilla between this and row *a*, recall the conditions in *Lebetus*. The lateral preorbital rows *c*¹ and *c*² are identical in both genera. On the dorsum of the head there is a correspondence in the reduced number and the arrangement of the papillae. *Lebetus* differs from *B. jeffreysii* in the disappearance of cephalic canals and their replacement by papillae of rows *a*¹, *u*¹, *i*¹, and the anterior part of *n*, together with a certain "condensation" of other rows (*d*¹, preoperculo-mandibular, opercular, and other series) and loss of rows *d* and *b*. The pattern of sensory papillae in *Lebetus* is obviously more specialized than that in *Buenia*, but the features present in both denote a greater affinity between these two gobies than is exhibited between *Lebetus* and other genera. In the persistence of cephalic canals and various rows of papillae, *Buenia* displays more ostensibly primitive characters than *Lebetus*. The former in addition retains the anterior pelvic membrane, is not so small as *Lebetus*, and does not show pronounced sexual dimorphism, although this does occur in growth of the first dorsal fin rays and probably in coloration of this fin. In the male genitalia, the testes are long and there is no free sperm duct. *B. jeffreysii* may accordingly show greater resemblance to the common stock from which the two are derived. The Mediterranean

species *B. reticulatus* (C. & V.) (= *B. affinis* (Kolombatovic)) is more removed from *Lebetus* in having a greater number of papillae especially in rows *b* and *d*, and a somewhat higher scale count (more than 33), than *B. jeffreysii* (Sanzo, 1911, pl. 9, figs. 9, 10; De Buen, 1930a). In Manx waters *B. jeffreysii* has an offshore distribution

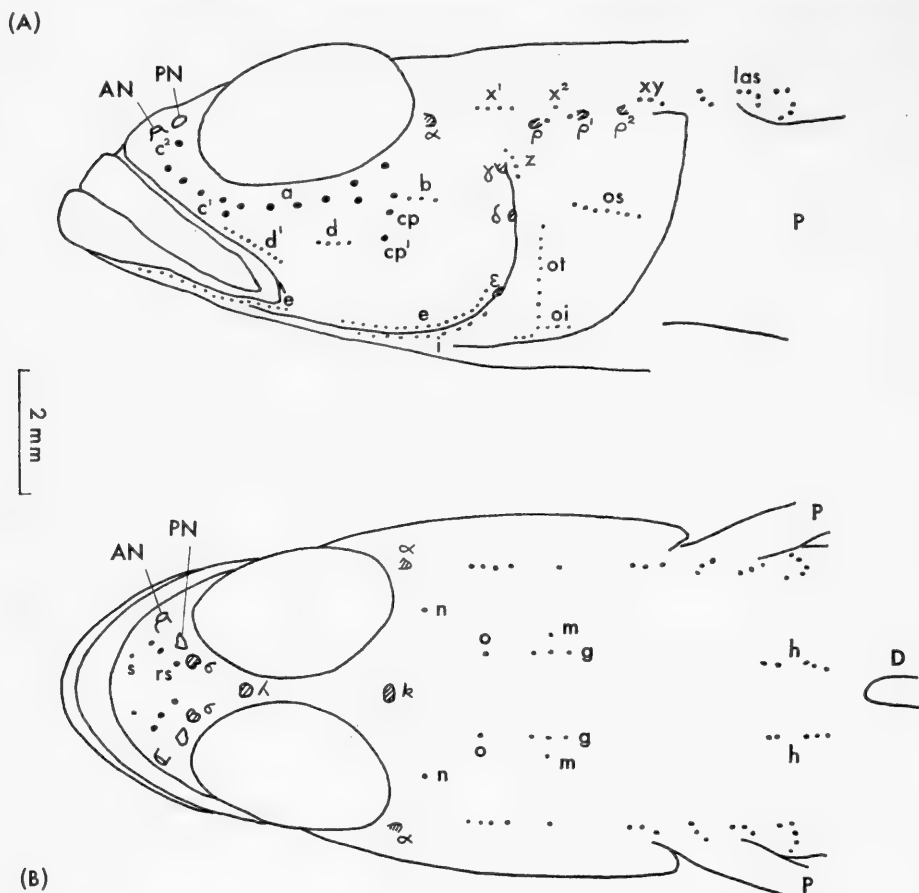


FIG. 21. Sensory papillae and orifices of cephalic canals in *Buenia jeffreysii*, male, 31 mm. standard length. (A) Lateral, (B) dorsal views of head. Abbreviations as in Fig. 7. Orifices of canals cross-hatched, with greek lettering as in Sanzo (1911).

like *Lebetus* and has even been taken from the same localities (see also Le Danois, 1910), but differences in precise habitat are perhaps reflected in the different body form and coloration (Holt & Byrne, 1903, fig. 4).

Some of the characters of *Lebetus* may be interpreted as adaptations to a mode of life involving intimate association with dead shells, nodules of calcareous algae, and stones. The small size of the fish is obviously related to this type of habitat, and the normal coloration may have cryptic value against a background of *Lithothamnion*. Te Winkel (1935) has discussed those anatomical features of the gobiid *Mistichthys*

luzonensis which may be correlated with the extremely small size of this species at maturity (standard length 10.0–11.0 mm.). Although *Lebetus* is diminutive, it is appreciably larger than *Mistichthys* and the only obvious comparable modification in this genus is the reduced size of the testis, to which may be related the form of the urogenital papilla as considered above. A more detailed examination of the viscera than was attempted in the present study would be needed to investigate this question. Reduction in number of sensory papillae has already been mentioned, and may be linked with small body size (Barlow, 1961b). The significance of loss of the cephalic canals is unknown; these are also lacking in *Lesueurigobius*, which attains 100 mm. in *L. friesii*, but are present in smaller forms such as *Odondebuenia*, *Buenia*, etc. Another feature of probable adaptive importance is the absence of the anterior pelvic membrane, since this is also missing in *Odondebuenia* which appears to have a similar habitat and which in addition exhibits almost complete separation of the pelvic fins. While the exact affinities of *Odondebuenia* await investigation, it seems likely that in view of the resemblances in arrangement of sensory papillae between this genus and *Gobius* the condition of the pelvis is derived from an original gobiid disc structure in response to environmental demands, and is not primitive as in the Eleotrids. The advantages conferred by the alteration of the pelvic disc in *Lebetus* and *Odondebuenia* are not obvious. The loss of the anterior membrane seems to have occurred independently in the evolution of the two genera as the exploitation of similar ecological niches proceeded in two areas from different stocks.

It must be stressed that the above phylogenetic conclusions may at present be regarded as tentative. Not only does the position of *Odondebuenia* remain doubtful, but the alignment of *Lebetus* with *Buenia* may well be affected by future work on the lateral line system of exotic gobies and faunistic exploration in little known areas, which together could disclose closer resemblances and intermediate forms between these and *Lebetus*.

SUMMARY

The teleostean genus *Lebetus* Winther 1877 (Percomorphi-Gobioidea) has been studied from new Irish Sea material dredged off the south of the Isle of Man, and from other examples, including types, in the collections of various British and Scandinavian museums. A redefinition of the genus includes the disposition of sensory papillae; there is a reduction in number of the latter, and cephalic canals and an anterior membrane to the united pelvic fins are lacking. Two species were previously recognized: *orca* Collett 1874 and *scorpioides* Collett 1874. Among the various criteria—coloration, meristic characters, body proportions—used in the past to distinguish these two species, it was found that only in coloration and development of the dorsal fins could the present *Lebetus* material be divided into two groups, termed *orca* and *scorpioides*. The former consisted entirely of males, nearly all maturing or mature, the latter of females and immature males. The conclusion is reached that there is only one valid species, by page priority *Lebetus orca*. A detailed account of the external anatomy and osteology of this species is provided.

In distribution *L. orca* is restricted to the European Atlantic boreal region, and a full list of records is provided in an appendix. The species is known chiefly from

coarse grounds, and has a wide bathymetric range from about 2 to 375 m. Investigation of gut contents, using a points system of assessment, shows that *L. orca* is exclusively predatory, feeding on small demersal animals which largely comprise crustacea and polychaetes. A number of endoparasites are listed. The male reproductive organs are peculiar in the relatively small size of the testis and the long free sperm duct; "seminal vesicles" are present. Sexual differences exist in the form of the urogenital papilla, which in mature males has an unusual terminal circlet of vascularized papillae. In Manx waters, the breeding season probably commences in March and may extend to August. 140 to 270 ripening oocytes have been counted in mature females. Sexual dimorphism is found in coloration, and size of dorsal and anal fins. Examination of scales indicates that duration of life may be at least two years, with sexual maturation at one or two years. Maximum total length recorded is 39.0 mm. Investigation of life history and growth in the Manx specimens was complicated by the high selectivity of the sampling gear employed.

In a discussion of the systematic position of *Lebetus*, it is shown that the skeleton is typically gobiid, and the arrangement of sensory papillae together with other features suggest that the nearest relative of this genus among the European gobies is *Buenia jeffreysii* (Günther). Previous grouping of *Lebetus* with two Mediterranean genera lacking an anterior pelvic membrane (*Odondebuenia* De Buen and *Cabotichthys* Whitley) is criticized. The validity of *Cabotichthys* is doubted, and the suggestion is made that loss of the anterior membrane in *Lebetus* and *Odondebuenia* occurred independently during their evolution and occupation of a similar habitat in different areas.

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APPENDIX

Distribution of *Lebetus orca*

A list of published and unpublished records known to the author is given below. A complete sequence of information is as follows : locality, number of specimens, sex, museum number, standard length + caudal fin length or total length in millimetres (mm.), depth of water in metres (m.), nature of ground, date of capture, and authority in the case of published records. When a number of records from the same locality or area are given in the one publication, these are separated by semicolons and the authority placed at the end. Abbreviations employed are : c., coarse ground ; cl., clay ; d., damaged ; gr., gravel ; h., hard ground ; *Lith.*, *Lithothamnion* ; m., mud ; midw., midwater ; *Mod.*, *Modiolus* ; n.d., no date ; s., sand ; sh., shells ; st., stones ; surf., surface ; t.l., total length ; w., weed.

ICELAND : Off S. and W. coasts, Eystra Horn to Breiðfjörður, "pelagic fry . . . rather rarely" (Tåning, 1940 ; Saemundsson, 1949).

FAEROES : Off N. coast, and Faero Bank, postlarvae (Tåning, 1940).

ROCKALL : On and near Rockall Bank, 1908 (Tåning, 1940).

NORWAY

Hemnefjord (Trondelag) : one ♂ (ZMO J4001), 23.0 + d.mm., July 1882 (Collett, 1885).

Søndfjord (Sogn og Fjordane) : Batalden, one ? ♂ (ZMO J4000), t.l. 22.0 mm., 375 m., summer 1875 (Lilljeborg, 1884 ; Collett, 1902).

Fedjefjord (Hordaland) : Herdla, two ♂♂ (ZMB 4174, 4175), 24.25 + d. and 26.0 + 7.25 mm., n.d. and 20 Aug. 1918.

Sørfjord (Hordaland) : Between Bruvik and Stamnes, one ♂ (ZMB 5294), 24.0 + 6.25 mm., 20-30 m., gr.s., 11 July 1953.

Hordaland : Bergen area, one, t.l. 29.0 mm. (Lilljeborg, 1884 ; Collett, 1902). Solsvig, one ♂ (ZMB 771), t.l. 31.0 mm., 56 m., sh.s., July 1899 (Collett, 1902). Herløvaer, one ♀ (ZMB 536), t.l. 28.0 mm., 37 m., sh.s., July 1898 (Grieg, 1899 ; Collett, 1902).

Hardangerfjord : Espevaer, one ♂ (ZMO J3999), 26.0 + 6.0 mm., 145-180 m., c.s., July 1873 ; Lyngholmen, one ♀ (ZMO J4021), 30.0 + 7.0 mm., 110 m., August 1873 (Collett, 1874, 1875a). Nordre Bratholmen (Hjeltefjord), one ♂, 23.5 + 7.0 mm., 50-100 m., sh.s., 30 Mar. 1903 ; Bognestrammen, one ♂ (ZMB 1966), 26.5 + 6.0 mm., 20-40 m., gr.s., 26 Apr. 1903 ; Guldholmen (Solsvik), one ♀ (ZMB 2009), 28.0 + 6.0 mm., 30-60 m., 25 Sept., 1903 ; Djupevik, one ♂ (ZMB 1893), 23.0 + 6.0 mm., 40-80 m., sh.gr.s., and one ♀, 27.5 + 5.0 mm., 20-60 m., sh.gr., 2 July 1909 ; Straumastein (Jondal), one ♂ (ZMB 1887), 18.5 + 4.0 mm., 100-200 m., sh.s., 15 June 1909 (Greig, 1913).

Stavangerfjord : Hvitingsø, one ♀ (ZMO J4020), t.l. 28.0 mm., 37 m., July 1872 (Collett, 1874, 1875a).

Rogaland : Egersund, one ♂ (ZMO J4023), 24.0 + 6.0 mm., 55 m., s., 12 Aug. 1880 (Collett, 1885).

SWEDEN

Kosterfjord (Göteborg) : May 1895 (Duncker, 1928). Sneholm, one, t.l. 35 mm., 100 m., st.; Säcken, one, t.l. 39 mm., 80 m., coldwater coral reef (Lönnerberg & Gustafson, 1935).

Gullmarfjord (Göteborg och Bohus) : August 1926 (Duncker, 1928). Flatholmen, two, 15-20 m., red algae (Lönnerberg & Gustafson, 1935).

DENMARK

Kattegat : Anholt Light NW. by W $\frac{1}{2}$ N., two, 45 m., 18 Apr. 1902 (Otterstrøm, 1912). Anholt, one, t. l. 16 mm., May 1902 (Petersen, 1919). SW. Anholt Harbour (56° 37' N., 11° 22' E.), fifty-four, upper and midw. in 18 m., 14 Apr. 1925 ; S. Anholt (56° 30.5' N., 11° 35' E.), sixteen, upper and midw. in 31 m., 14 Apr. 1925 ; E. Store Middelgrund (56° 33.5' N., 12° 13' E.), one, midw. in 48 m., 8 Apr. 1925 ; 56° 15' N., 11° 53' E., nine, 13.0-17.0 mm., upper and midw. in 25-26 m., m.s., 20/21 Apr. 1925 (Johansen, 1925). Hesselø, about twenty young, August 1918 (Petersen, 1919). Yderflakket (between Sjaellands Odde and Hjelmen), one ♂ (ZMC 91), 14.4 + 4.0 mm., 11 m., st.gr.w., 18 Aug. 1876 (Winther, 1877). Sjaellands Odde, one ♂ (ZMO 89), 14.5 + 4.5 mm., 22 May 1913.

Great Belt : "fairly often single or a few young specimens", c. 18-20 m. (Petersen, 1919). Tørrsø (N. of Fünen), June 1912 ; Oddens Havn, May 1913 (Duncker, 1928). SE. Romsø (55° 30' N., 10° 52' E.), five, midw. in 30 m., 16 Apr. 1925 (Johansen, 1925). Kerteminde, one, t.l. 15.0 mm., 4 m., 19 May 1904 ; Nyborg, "small young", Aug. 1917 ; E. Palegrund, two, t. l. : 3.5 and 4.5 mm., 6 Aug. 1917 ; E. Vresen's buoy, one, t. l. : 5.5 mm., 24 m., 19 Sept. 1917 (Petersen, 1919).

Fehmern Belt : SE. Staberhuk (54° 22' N., 11° 23' E.), one, midw. in 23 m., 17 Apr. 1925 (Johansen, 1925).

BRITISH ISLES

Northumberland : Off Alnmouth (55° 24' N., 1° 31.5' W.), larvae, 8 Sept. 1925 (Ehrenbaum *et al.* (1929) attribute this record to Schnakenbeck (1928) but a search through this paper has failed to reveal it).

Clyde Sea Area : Kilbrennan Sound, one ♂ (BMNH 90.10.20.9-10), t.l. 37.5 mm., 22 Mar. 1888 (Günther (1888) as ♂ *Gobius jeffreysii* ; Collett, 1896). Between Scalpsie Bay and Cock of Arran (55° 44' N., 5° 11' N.), one ♂, 26.0 + 8.0 mm., 135-160 m., m.; Largs Channel (55° 45' N., 4° 54' W.), one ♀, 29.0 + 7.0 mm., 35 m., h.; Firth of Clyde (55° 41' N., 5° W.), one ♂, 27.0 + 7.0 mm., 93 m., m. (Patience, 1906). E. Cumbrae, off Cock of Arran, in over 146 m. (Elmhirst, 1926).

Ireland : Inislyre Harbour, Clare Island (Mayo), one, 9 m., sh.st., May 1909 (Farran, 1912). Ballynakill Harbour (Galway), several, including two ♂♂, 12.0 + d. and 16.0 + 4.0 mm., and two ♀♀, 10.5 + d. and 17.0 + 5.0 mm. (BMNH 1903.4.14.4-7), 2-5.5 m., sh.st. *Lith.*; 30 mi WNW. Cleggan Head (Galway), one, ♀♀, 135 m. (Holt & Byrne, 1903).

Irish Sea : Up to 2 mi off Bradda Head (Isle of Man), eight, t.l. 3.5-8.0 mm., at 4.5-7.2 m., 18 May-19 July 1939 (Bal, 1940a). 2½ mi WSW. Chicken Rock (Isle of Man), one, 37 m., sh., 29 May 1947 ; 1½ mi SW. by W. Chicken, one, 37 m., sh.gr.m., 5 Aug. 1947 ; 2 mi. WSW. Chicken,

one, 37 m., sh., 11 Sept. 1947; $3\frac{1}{2}$ mi WNW. Chicken, four, 49 m., sh.s., 6 Aug. 1948; 3 mi SW. by S. Chicken, two, 42 m., sh., 21 Sept. 1948; 3 mi W. 5° N. Chicken, one, 51 m., sh.st., 21 Sept. 1948; $4\frac{1}{2}$ mi ESE. by 5° E. Langness (Isle of Man), one, 35 m., st.*Mod.*, 24 Sept. 1948; $6\frac{3}{4}$ mi ESE. by 5° E. Langness, one, 42 m., sh.st.gr., 25 Sept. 1948; 3 mi ESE. Douglas Head (Isle of Man), three, including ♀ 18.0 + 5.75 mm., 29 m., sh.*Lith.*, 22 Nov. 1948; $1\frac{1}{2}$ mi WSW. Chicken, one ♂ (PEM), 26.5 + 6.5 mm., 44 m., m.s., 10 May 1949; 4 mi SW. Chicken, one ♀ (PEM), 28.0 + 6.2 mm., 40 m., sh.st. (Jones, 1949, 1950, 1951). Five mi E. Douglas Head, one ♂, 23.5 + 6.5 mm. and one ♀, 23.5 + 5.5 mm., 33 m., sh.*Lith.*, 22 Sept. 1948; $\frac{1}{4}$ mi NE. Calf Stack (Isle of Man), one ♂, 26.0 + 6.8 mm., sh.st., 7 May 1957; $\frac{3}{4}$ –1 mi N. Calf Island, eleven ♂♂, 20.5 + 5.5 to 26.75 + 7.25 mm., and nine ♀♀, 23.75 + 6.25 to 28.0 + 6.5 mm., 18–35 m., sh.st.*Lith.*, 25 Mar. 1958 to 31 Oct. 1960; $1\frac{1}{4}$ mi N. by E. Calf, one ♀, 25.0 + 6.0 mm., sh.m., 4 Apr. 1960; 4 mi S. Spanish Head (Isle of Man), one ♀, 28.0 + 7.0 mm., 53 m., *Mod.*, 11 Mar. 1958; Off Aldrick Bay (Isle of Man), two ♀♀, 23.5 + 5.5 and 25.75 + 6.5 mm., 20 Oct. 1958 and 5 Nov. 1959; $\frac{1}{4}$ mi W. Bradda Head, two ♂♂, 23.25 + 6.5 and 30.0 + 7.5 mm., one ♀ 23.0 + 6.0 mm., 25 Nov. 1958, and two ♀♀, 17.0 + 4.75 and 24.5 + 6.5 mm., 14 Apr. 1959, 27 m., sh.st.m.s.w.; $2\frac{1}{2}$ mi S. Perwick Bay (Isle of Man), four ♂♂ (including BMNH 1961.10.17.1, 3), 23.0 + 6.2 to 28.0 + 6.3 mm., one ♀ (BMNH 1961.10.17.2), 29.0 + 7.0 mm., 10 Feb. 1959, and two ♂♂, 17.0 + 4.5 and 20.0 + 5.0 mm., 16 Nov. 1959, 35 m., sh.st.gr.*Lith.*; $\frac{1}{4}$ mi W. Port Erin Breakwater (Isle of Man), one ♂, 15.75 + 4.4 mm., 9–27 m., st.gr.w., 28 Sept. 1959; W. Calf Sound, one ♂, 23.0 + 5.75 mm., sh.st.m.s., 29 Sept. 1959; Aldrick Bay, one ♀, 14.5 + 4.0 mm., 18 m., sh.gr., 2 Oct. 1959; $2\frac{3}{4}$ mi W. Calf Sound, one ♀, 26.75 + 6.75 mm., sh.st.gr., 16 Oct. 1959; $\frac{1}{2}$ mi N. Aldrick Rock, one ♂, 24.25 + 5.75 mm., sh.m.s.w., 9 Dec. 1959; 4 mi SW. Chicken, one ♀ (BMNH 1961.10.17.4), 28.25 + d. mm., 51–58 m., sh.gr., 10 Feb. 1960; $6\frac{1}{2}$ mi W. Sound, one ♂, 22.0 + 6.0 mm., and two ♀♀, 25.25 + d. and d. mm., 49–64 m., sh.gr.m.s., 3 May 1960; 5 mi W. Sound, one ♂, 24.5 + 6.75 mm., 55 m., 8/14 June 1960; $9\frac{1}{2}$ mi W. Port Erin, one ♂, 23.5 + 6.0 mm., 60–65 m., sh.m.s., 8 July 1960; $1\frac{1}{4}$ mi N. Chicken, one ♂, 26.0 + 6.0 mm., 42 m., sh. and abundant *Flustra*, 3 Feb. 1961; 3 mi WSW. Chicken, one ♂ (BMNH 1961.10.17.5), 25.0 + 6.5 mm., 42 m., sh., 10 May 1961; also from Manx area, exact localities unrecorded, three ♂♂, 16.0 + 4.5 to 26.5 + 7.0 mm., and three ♀♀, 22.0 + 5.0 to 28.5 + 7.25 mm.

Western English Channel: 6 mi W. Rame Head (Cornwall), one, t.l. 11.0 mm., midw. in 48 m., 24 Oct. 1913 (Clark, 1914). Rame Penlee, one, 6.5 mm., 13 m., 3 July 1919; $5\frac{1}{2}$ mi WSW. Rame, one, 5.0 mm., 38 m., 21 July 1919; $4\frac{3}{4}$ mi S. by W. Rame, two, 4.0 and 7.0 mm., 31 July 1919; $3\frac{1}{4}$ mi NE. by E. Eddystone, one, 6.0 mm., midw. in 55 mm., 5 Aug. 1919; $3\frac{3}{4}$ mi S. 14 W. Rame, two, 5.0 and 6.0 mm., 41 m., 5 Aug. 1919; 4 mi S. 17 W. Rame, one, 7.0 mm., midw. in 41 m., 8 Aug. 1919; $\frac{1}{2}$ mi E. Eddystone, two, 6.0 and 7.0 mm., 37 m., 8 Aug. 1919; 5 mi SW. by W. Rame, one, 5.0 mm., 50 m., 11 Aug. 1919; 20 mi S.W. 5 W. Eddystone, eleven, 5.0 to 12.0 mm., surf. and midw. in 75 m., 9 Sept. 1919 (Clark, 1920). Off Plymouth Sound ($50^{\circ} 17'$ to $18^{\circ} 30'$ N., $4^{\circ} 10'$ to 11° W.), three at 3.8–18.1 m., 13/27 June 1924; 10 mi SW. Eddystone, eight, 17 June 1924, and two, 15 July 1926, at 12.4–57.8 m.; 5 mi N. Eddystone, eighteen, at surf. to 52 m., 25 June 1924/30 June 1926; c. $2\frac{1}{2}$ mi N. Eddystone, six, at 14–30 m., 17/19 June 1925; 2 to 3 mi E. Eddystone, one hundred and thirty, at 3.3–43.1 m., 1 July 1925/22 Sept. 1926; other postlarvae recorded May/Oct. and Dec. 1927; July/Oct. 1929; June/Oct. 1930/34; May, Sept. and Oct. 1935; June, July and Oct. 1938; Aug. 1939 (Russell, 1926*a, b*, 1930*a, b*, 1935, 1936, 1939, 1940). 200 to 300 yds. (4 to 6 cables) NNW. Eddystone, occasional, sh.gr. (Marine Biological Association, 1957; ground described by Smith, 1932). Falmouth Harbour (Cornwall), one ♀, t.l. 21.0 mm., 33 m., sh., 13 July 1897 (Holt & Byrne, 1898). 34 to 47 mi S. 17° to 27° W. Eddystone, one, t.l. 33.0 mm., 90–97 m.; 46.4 mi S. 25 W. Eddystone, one, t.l. 31.0 mm., 91 m., sh.st.gr.s. (Crawshay, 1912).

FRANCE

Western Channel: estuaries of Morlaix and Penzé, near Roscoff (Finisterre), fifteen, 10.0 + 3.0 to 17.5 + 4.5 mm., 5–8 m., "maerl" (Le Danois, 1910, 1913). Baie de Morlaix, Roscoff, "rare", 4–15 m., sh.maerl (Cantacuzene, 1956). Off NW. Finisterre ($48^{\circ} 40'$ N., $5^{\circ} 4'$ W., and

48° 43' N., 4° 45' W.), one, t.l. 7.0 mm., in 113 m., s., 7 May 1906, and two, t.l. 11.0 and 12.0 mm., in over 100 m., st., 19 Sept. 1910, respectively (Fage, 1918; Schmidt, 1912).

Bay of Biscay: Sables d'Olonne (46° 27' N., 6° 30' W.), two, t.l. 24.0 mm., 166 m., m.s., 20 July 1886 (Collett, 1896).

DOUBTFUL RECORDS

Fage (1918) regarded larval fishes from the Straits of Gibraltar (Atlantic) as possibly referable to *Gobius scorpioides*, at the following stations: 35° 45' N., 5° 59' W., sh.st., in 58 m., 21 Feb. 1909; 35° 50' N., 6° 3' W., st., in 490 m., 21 Feb. 1909; 35° 57' N., 6° 0' W., m., in 275 m., 23 June 1910; 35° 51' N., 5° 58' W., clay, in 343-720 m., 8 Sept. 1910. Station details are from Schmidt (1912).



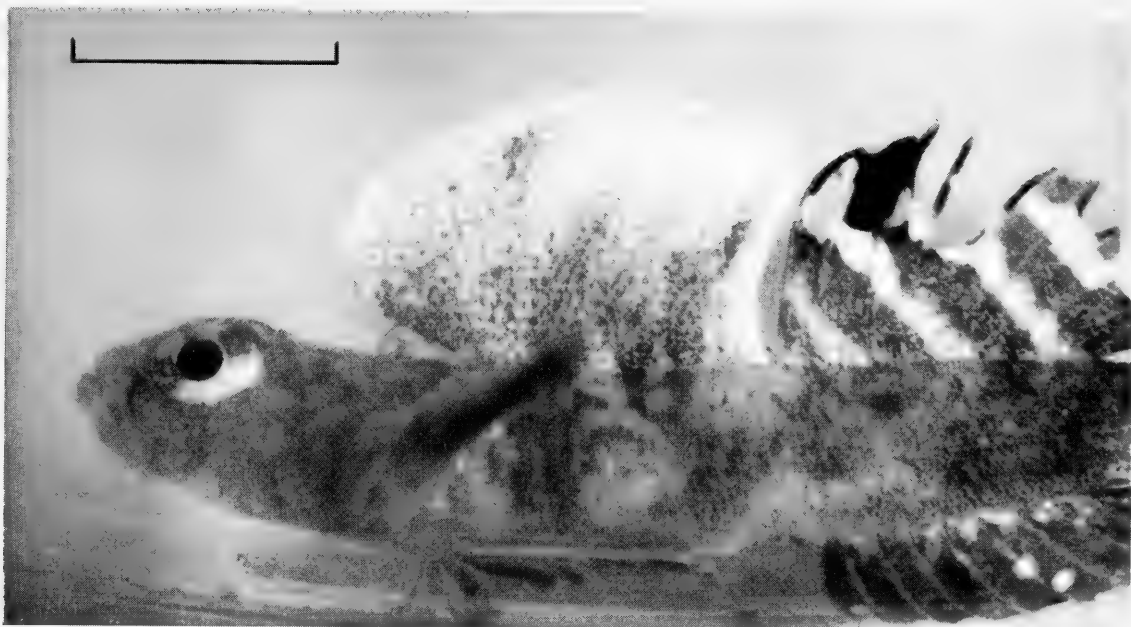


PLATE I

Male *L. orca* (BMNH 1961.10.17.5) with extended first dorsal fin. From colour-transparency by Mr. D. J. Slinn. Scale 5 mm.

THE FRESHWATER GASTROPOD MOLLUSCS OF WESTERN ADEN PROTECTORATE

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THE FRESHWATER GASTROPOD MOLLUSCS OF WESTERN ADEN PROTECTORATE

C. A. WRIGHT

IN the spring of 1962 a collection of freshwater gastropod molluscs was made during the course of an investigation into the transmission of human schistosomiasis in the Western Aden Protectorate. Material was collected in four areas, Abyan, an irrigated part of the coastal plain about 30 miles east of Aden, the Wadi Yeshbum in Upper Aulaqi near the border with the Eastern Protectorate, the Wadi Hatib south of Nisab, also in Upper Aulaqi and at Museimir in Haushabi, on the Wadi Tiban near to the Yemen border.

I am indebted to Dr. C. R. Jones, the Health Adviser, Aden Protectorate, and to Dr. J. Markham, Assistant Health Adviser, Western Aden Protectorate, for the facilities to carry out this work and for practical help in the field. I also wish to thank Mr. Andrew Fuller, Assistant Adviser, Upper Aulaqi, for his help and Mr. D. Claugher for his assistance both in the field and in the laboratory. The work was made possible by grant number E3650 from the U.S. Public Health Service.

HISTORICAL

Paladilhe (1872) published descriptions of several land and freshwater molluscs from the area around Aden and his work provided the basis for subsequent reviews by Jousseume (1889) and Ancey (1906), both of whom added further species to the known molluscan fauna of the area. Connolly (1941) reported on the non-marine mollusca collected by the British Museum (Natural History) expedition to Yemen and the Western Aden Protectorate and included an account of specimens collected by the Lord Wakefield expedition to the Hadhramaut. At the end of that paper Connolly gave a faunal list for Southern Arabia, based on Ancey's work but with additions. In recent years the only references to freshwater molluscs in South-west Arabia have been in reports of schistosomiasis surveys by Petrie & Seal (1943), Kuntz (1952), Ayad (1956), Azim & Gismann (1956) and Farooq (1961) but only the first of these was directly concerned with the Western Aden Protectorate.

Topography of the areas visited

The general topography of South-west Arabia was described by Scott (1939). The Western Aden Protectorate lies at the western end of the southern shore of the Arabian peninsula and extends inland for several hundred miles at its border with the Eastern Protectorate. There is a wide coastal plain of desert, broken in some places by barren outcrops of hills, and inland the folded ridges of mountains reach

heights of over 7,000 feet. To the north lie the mountainous areas of Yemen and to the north-east is the edge of the vast desert of Rub' al Khali.

Throughout most of the region bodies of permanent, fresh, surface water are rare. Rainfall is erratic in the lower hills, sometimes torrential, sometimes absent and much of the land surface is porous. In the highland areas there are more regular, heavy monsoon rains during which rivers flow through the inland valleys but few of them reach the sea except when occasional flash-floods descend, scouring the beds of the wadis which dissect the coastal plain. Cultivation in the uplands is mostly confined to valleys where the water table is high and wells provide a barely adequate water supply. In some of these areas springs occur, and short, permanent streams run above ground for distances varying from a few hundred yards to several miles



Map showing approximate positions of the areas in which collections were made.

before disappearing. This is the situation in the Wadi Hatib near Nisab in Upper Aulaqi State. Near the lower (north) end of the valley at Ma'rbaḥ there are a number of small springs whose waters spread out to form a marshy area in which dense thickets of large reed-mace (*Typha*) thrive. In the rivulets and pools of this marsh there are many fish, frogs, aquatic insect larvae and snails. Further up the valley at Rassaiṣ there are one or two large springs which give rise to a clear gently flowing stream with deep, rocky pools in which fish are abundant and freshwater turtles also live. Snails are common in the shallow parts of the stream, also in a rock pool not connected with it in a cleft of the cliff above the main spring. Higher up the wadi at Tarbak a small river rising from a spring has cut a gorge in the otherwise barren floor of the valley. During its course of about a mile this stream passes through wide, almost still pools then runs over shallow, shingled beds before flowing

rapidly through a narrow, rocky channel and down a waterfall into a deep pool and on down the gorge. In this short but varied course there is a wide variety of habitats and this is reflected in the occurrence of a richer snail fauna than was found anywhere else in the Protectorate.

Further to the east in Upper Aulaqi State is Wadi Yeshbum, a relatively fertile valley with a high water table. A spring near As Sufal gives rise to a small, shallow stream which flows several miles toward the escarpment marking the boundary between the Eastern and Western Protectorates. Near Said and Yeshbum there are narrow gorges entering the main valley and in some of these there are deep rock pools which persist for long periods and may even be permanent.

In complete contrast to this terrain is Abyan, a low-lying irrigated district in the coastal plain about thirty miles east of Aden. This irrigation scheme owes its existence to the Wadi Bana, one of the few permanent rivers which reaches the coastal plain, and the Wadi Hasan which, although not wholly permanent has sections where springs give rise to small perennial streams in the river bed. Near the north end of the district the two wadis almost converge and the irrigation works have provided a link so that water from either source can be fed into the canal system. Near to this point is a permanent spring, independent of either wadi, whose water provides irrigation for vegetable gardens in the near-by village of Bateis. The general irrigation system is only in use seasonally and the principal snail habitats appear to be confined to a few parts of the permanent, natural waters in the wadis and the spring.

The Wadi Tiban at Museimir in Haushabi was the only other locality visited and it is in some respects intermediate in character between the habitats in Upper Aulaqi and those in Abyan. There is a permanent shallow stream flowing over the shingle bed of the wadi in a low-lying valley surrounded by hills. Despite its lower altitude (about 500 feet) the snail fauna at Museimir is the same as that at As Sufal in the Wadi Yeshbum (about 3,000 feet).

Family *PLANORBIDAE*

Biomphalaria rueppelli (Dunker)

(Pl. I, 1-8)

Planorbis rueppellii Dunker, 1848, p. 42.

Planorbis arabicus Melvill & Ponsonby, 1896, p. 3, Pl. I, figs. 15-17.

Biomphalaria arabica Connolly, 1941, p. 33.

Biomphalaria boissyi arabica Kuntz, 1952, p. 25.

Biomphalaria sp. (in part) Ayad, 1956, p. 90.

UPPER AULAQI: Wadi Yeshbum at Marbūm, As Sufal and Sumayfah, either in rock pools or gently flowing water, 3,000-3,200 ft.

Wadi Hatib, Ma'rbah and at Tarbak and Rassais, in streams, about 4,000-4,500 ft.

HAUSHABI: Museimir, in the Wadi Tiban in shallow, flowing water, about 500 ft.

The whorls of the shell are flattened above and bluntly angled beneath, the innermost are deeply sunk on the upper surface and the umbilicus is narrow. Apart from a well-marked spiral sculpture on most of the specimens this material does not differ

significantly in shell-form from material collected in the highlands of Ethiopia (Wright & Brown, 1962). The largest specimen found in Aden (at Sumayfah) measured 10.5 mm. in maximum diameter, 3.2 mm. umbilical diameter and 4.1 mm. in height. These dimensions are almost the same as those of the holotype of *B. arabica* (10.8, 3.65, 4.0).

The mantles of all the specimens dissected were uniformly darkly pigmented and without distinct markings. The penis sheath and preputium are approximately equal in length in most individuals but in a few the sheath is a little shorter than the preputium. The number of primary prostate diverticula is at least twelve in adult snails.

The mesocones of the lateral radula teeth are all triangular; none of the arrow-head type were seen. Subdivision of the marginal ectocones is general but in some radulae the marginal ectocones may be undivided in one or two longitudinal rows (Fig. 5).

This species is widely distributed in South-west Arabia and is the dominant basommatophoran in areas away from the coast. The type locality for *B. arabica* is Dhofar in the Hadhramaut and Connolly (1941) records the species from several localities in the Western Aden Protectorate and Yemen. Through the kindness of Dr. Naguib Ayad of the Ministry of Public Health, Cairo, I have been able to examine shells of the specimens which he collected in Yemen and there is no doubt that his material also belongs to this species. Kuntz (1952) treated *arabica* as a sub-species of *B. alexandrina* (= *boissyi*) but the present study shows that it is correctly placed in the *pfeifferi* group. Jousseau (1889) referred to the young planorbid recorded by Paladilhe (1872) from alluvial debris at Kursi, near Aden, as belonging to the *adowensis* group and it has recently been shown that *B. adowensis* is almost certainly not distinct from *B. rueppelli* (Wright & Brown, 1962).

B. rueppelli is found in practically every body of permanent fresh water in the part of Upper Aulaqi which was visited. The snails reach maturity at a relatively small size and lay large numbers of eggs. The population density in some rock pool habitats is very great and, with the large numbers present and their wide distribution, it is surprising that infection with *Schistosoma mansoni* is not a more serious public health problem than it appears to be.

Gyraulus convexiusculus (Hutton)

(Pl. I, 9-17)

Planorbis convexiusculus Hutton, 1849, p. 657; Connolly, 1941, p. 36.

UPPER AULAQI: Sumayfah, Wadi Yeshbum, from deep rock pools and shallow, flowing water, about 3,200 ft.

Tarbak, Wadi Amhadu (part of Wadi Hatib), from a slow-moving part of the stream, abundant on aquatic vegetation.

LOWER YAFI: Nabwa spring, Bateis, Abyan, three very young specimens, probably belonging to this species.

The shells are small, flattened and the whorls do not increase in diameter so rapidly as they do in the common African species, *G. costulatus*. The mean dimensions of a

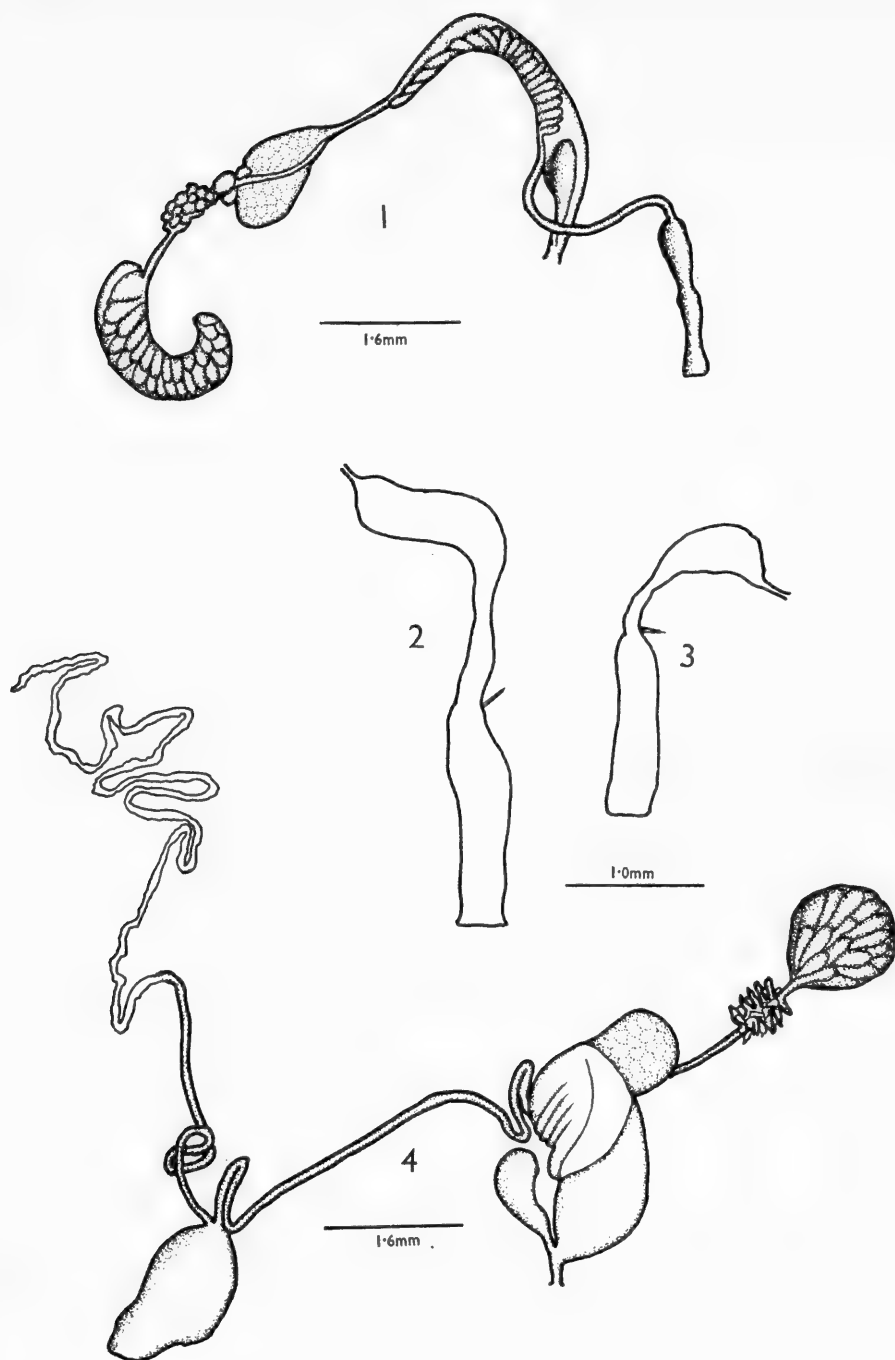


FIG. 1. *Gyraulus convexiusculus*. Complete reproductive system.

FIGS. 2 & 3. *Bulinus reticulatus*. Male copulatory organs of two individuals from Rassais.

FIG. 4. *Ancyclus fluviatilis*. Complete reproductive system of specimen from Tarbak.

small sample of adult specimens from Tarbak are, diameter 4.3 mm., umbilicus 1.6 mm. and height 1.1 mm. There is no obvious angulation of the whorls and the aperture is roughly oval. There is a superficial, somewhat coarse spiral sculpture on most of the specimens, recalling the appearance of *G. kigeziensis nyanzae* Mandahl-Barth 1954.

Anatomically *G. convexiusculus* differs from *G. costulatus* in the less compact arrangement of the accessory genital glands, a reflection of the differences in shell-form between the two species (Text-fig. 1). The penis sheath and preputium are roughly equal in length but the proximal dilatation of the penis sheath is wider than the maximum diameter of the preputium. The structure of the penial stylet is the same as that described for *G. costulatus* (Wright, in press). The prostate in *G. convexiusculus* is long and has as many as eighteen primary diverticula without marked secondary branching. The radula teeth are very small (Text-fig. 6) and the cusps of the laterals are longer and more lanceolate than those of *G. costulatus*. There are six tricuspid laterals in each half-row, about five transitional teeth which resemble the laterals except in the division of the ectocone and about six marginals. The marginals have the ecto- and endocones divided into two cusps each, resulting in five-cusped teeth instead of the seven-cusped marginals in Angolan *G. costulatus*.

Connolly (1941) recorded this species from the Hadhramaut at Hureidha, Wadi Jedd. The present material is so close to a series collected at Kandahar (Afghanistan) by Hutton (possibly the type material, B.M. (N.H.) collection number 56.9.15.79) that there is no reason to consider it to be a separate species unless subsequent anatomical studies of topotype material reveal any marked differences.

Bulinus sericinus (Jickeli)

(Pl. II, 1-4)

Isidora sericina Jickeli, 1874, p. 194, Pl. III, fig. 2.

Bulinus truncatus Connolly, 1941 (in part), p. 33.

UPPER AULAQI: Tarbak, Wadi Amhadu (part of Wadi Hatib), from rushes and emergent grasses in an almost still pool, also on stones and rocks in a narrower, more rapidly flowing part of the stream, about 4,500 feet.

A large sample was collected and it includes a wide range of shell forms. Wright & Brown (1962) have discussed variation in this polymorphic species from the Ethiopian highlands and this material from Aden includes most of the forms described. The majority of the smaller specimens, some smooth-shelled, with or without inflated whorls, some strongly ribbed (var. *harpula* Pollonera), were collected on vegetation in an almost still part of the stream while larger individuals, most of them with exserted spires (*shackoi* Jickeli) were more abundant on rocks in rapidly flowing water.

Anatomically the Aden material differs from the Ethiopian populations studied earlier in that the majority are aphyallic. This condition was found in only one of a large number of Ethiopian specimens. Euphallic individuals in the Tarbak sample have a copulatory organ similar to that described by Mandahl-Barth (1960) for *B. mutandensis*. The penis sheath is longer than the preputium and, at its maximum

diameter, it is also a little wider. The sheath is regularly banded with dark rings, the epiphallus is short and, in one specimen a slight proximal dilatation of the epiphallus was seen. The radula teeth of *B. mutandensis* are described by Mandahl-Barth as about twice the size of those of *B. truncatus* but the teeth of the specimens from Tarbak (Fig. 7) do not differ significantly from those of Ethiopian *B. sericinus*.

Ayad (1956) mentioned that Mandahl-Barth identified all of his bulinids from the highlands of Yemen as *B. sericinus* (Jickeli) and, after examining the Yemeni specimens named as *B. truncatus* by Connolly (1941), I think that this is a valid action. Connolly's material was all found between altitudes of 7,900 and 9,300 ft. A sample of six specimens in the collection of the British Museum (Natural History) collected by Dr. Haythornthwaite from Lower Yafai do not have an exact locality and the altitude at which they were found is not known. At the present time it seems that my sample from Tarbak is from the lowest altitude yet recorded (about 4,500 ft.) for this highland species.

The role of *B. sericinus* as an intermediate host for schistosomes is not yet certain. One of the specimens from Tarbak shed schistosome cercariae about two weeks after it was collected but the species of parasite has not been identified. A few snails from this sample were exposed to miracidia of *Schistosoma haematobium* hatched from a urine sample collected at Said but no cercariae were produced.

Bulinus reticulatus Mandahl-Barth 1954

(Pl. II, 5-8)

Bulinus truncatus (var.) Connolly, 1941, p. 37.

UPPER AULAQI: Wadi Yeshbum at Marbum, near Said, in rock pools in a narrow gorge, about 3,200 ft.

Rassaiss, Wadi Hatib, south-east of Nisab, in a moderate-sized pool in a cleft of a small cliff at the head of a gully, about 4,000 ft.

The shells of these specimens compare well with those of a small sample from the type locality, Kisumu in Kenya. Those from Said tend to have the spire more exerted and those from Rassaiss are uniformly globular with a pronounced spire. The largest specimen collected (from Said) had a shell-length of 6.1 mm., aperture length of 3.7 mm. and maximum width of 4.0 mm. The mean length of twenty shells from Said was 4.9 mm. and from Rassaiss 5.1 mm. The mean ratio of shell-length to aperture length is 1.6 in both samples but the more globular specimens from Rassaiss, have a lower length/width ratio (1.30) than the narrower specimens from Said (1.42).

The most marked macroscopic feature of the shell in this species is the broadly reflexed, straight collumella and wide umbilicus. On dead shells collected at Said there is a very strongly marked reticulate sculpture which can be seen clearly with a hand lens but fresh, translucent shells require more careful examination.

Preliminary observations on the anatomy of this material showed that it differed in several respects from the descriptions published by Mandahl-Barth (1954 & 1957). Three specimens from Kisumu, Kenya, were therefore dissected for comparison. The mantle in the snails from Aden appears uniformly black, due to the dense and

even distribution of chromatophores, and it has a pale grey margin which is often reflexed over the edge of the aperture; the mantle markings of the Kisumu specimens are regular black spots and blotches on a light grey ground. The male copulatory organ is very large relative to the size of the animals, about 3.5–4.0 mm. total length in a 5 mm. shell (Text-figs. 2 and 3). According to Mandahl-Barth the preputium is exceptionally big and it is wider and longer than the sheath. In material from both localities in Aden the sheath is a little longer than the preputium and its maximum diameter is at least equal to that of the distal part. The specimens from Kisumu have the sheath and preputium roughly equal in length and in only one of the three dissected was the preputium conspicuously wider than the sheath. The epiphallus is short. Mandahl-Barth refers to the radula teeth of *B. reticulatus* as very small and with the endo- and mesocones not completely separated. The teeth of the Kenyan specimens are certainly small and the cusps are fine and lanceolate but there is scarcely any fusion of the inner and middle cusps of the laterals (Text-fig. 9). The Aden specimens, on the other hand, have larger teeth, the mesocones of the laterals are very big and spatulate and the endocones are reduced to small points on the inner margins of the mesocones (Text-fig. 8). There are eight or nine laterals in the Aden radulae and twelve to fourteen marginals while those from Kisumu have six or seven laterals and sixteen to eighteen marginals. The marginals of the Kenyan specimens are more delicately pectinate than those from Aden.

B. reticulatus in East Africa is known only from temporary habitats and it seems likely that the pools at Said and Rassais may not be permanent. Water originating from some springs in the Wadi Hatib has a high mineral content which results in a white crust being deposited around the edge of drying pools. Well-water from Nisab has a total dissolved solids content of about 1750 p.p.m. of which 480 p.p.m. are total hardness and about 550 p.p.m. are sodium chloride. Analysis of a small sample of water from the pool at Rassais (carried out by the laboratory of the Government Chemist, London) showed total dissolved solids of only 200 p.p.m. of which 40 p.p.m. were total hardness and 60 p.p.m. sodium salts. This suggests that the pool is filled largely by rainwater rather than from a spring and it is almost certain, therefore, to dry out periodically. The only other animals found in the Rassais pool were a single pair of waterbeetles, *Hydaticus jucundus* (Reiche) and a number of anostracan crustacea, kindly identified for me by Dr. J. Harding as *Streptocephalus neumanni* Thiele; both of these species are characteristic elements of ephemeral waters.

Connolly (1947) described in some detail a large sample of what he considered to be a variety of *B. truncatus* from Al Bahr in the Hadhramaut and he mentioned that they were so different from the typical form that they might be considered to be a separate species. These specimens have been re-examined and proved to be *B. reticulatus*. The isolated and obscure habitats in which the snails occur at Rassais and Said, also their probably temporary nature, suggest that this species is likely to be overlooked in any routine survey for medically important snails. It was because the Marbum pools at Said were reputed to be the local source of infection with urinary schistosomiasis that they were visited and the pool at Rassais was found only by chance. From three records for the species in Southern Arabia it is impossible to guess at its distribution but it is likely to be found in the middle heights throughout

the Protectorate and possibly in Yemen also. Epidemiological evidence points to this snail as the intermediate host of *Schistosoma haematobium* at Said and specimens from Rassais have proved to be excellent hosts in the laboratory for the Said strain of parasite. The snails breed easily in the laboratory, the egg-masses are relatively large for a small bulinid with up to fourteen eggs in each and the size at hatching is smaller than in *B. forskali* but the "infant mortality" rate is lower.

Bulinus beccari (Paladilhe)

(Pl. II, 9-14)

Physa beccarii Paladilhe, 1872, p. 23, Pl. I, figs. 7 & 8.

Bulinus forskalii Azim & Gismann, 1956, p. 436, figs. 18, 19.

FAHDLI: Wadi Hasan at Dirgag, Abyan, in shallow, running water with dense aquatic vegetation and a sandy bottom.

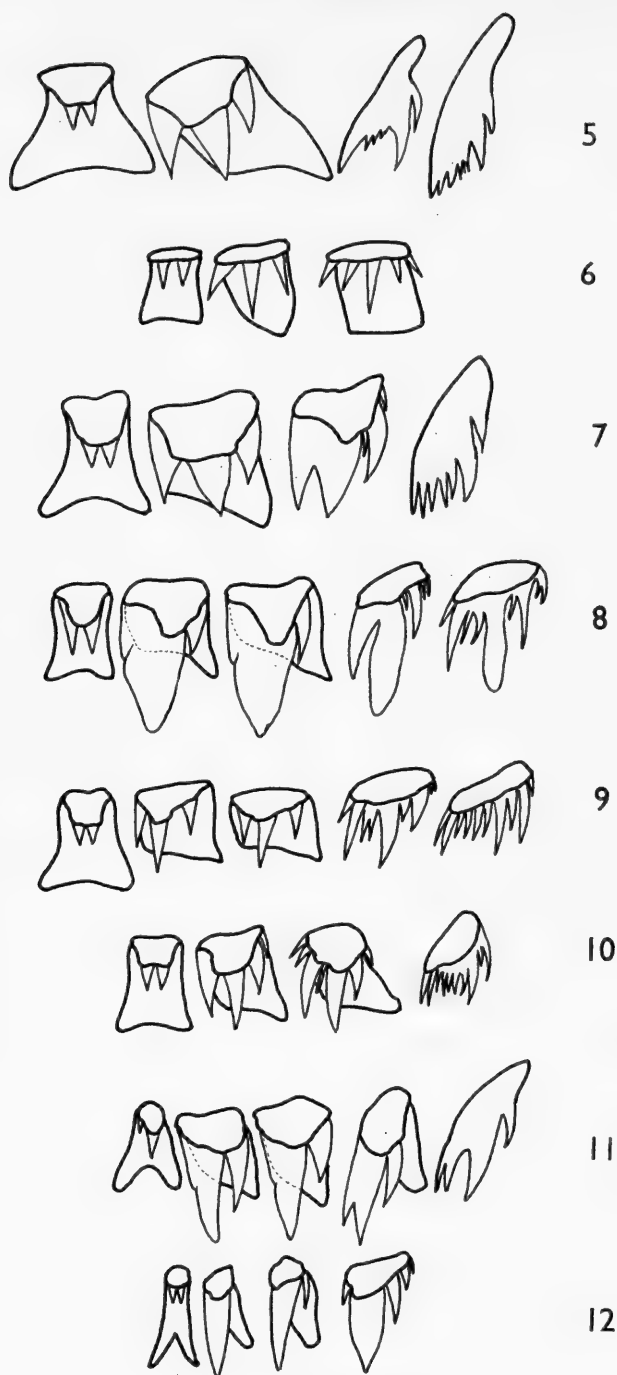
LOWER YAFAI: Bateis, Abyan, in the Nabwa spring in cool, relatively deep gently flowing water on *Ceratophyllum* and other aquatic plants, also a single living specimen and one dead shell in the Wadi Bana under a stone in shallow, fast-running water.

The shell is high-spired and elongate, translucent white, without marked ribbing and with a slight carination forming an ill-defined shoulder on the earlier whorls. The columella is slightly twisted at its upper end and its margin is reflexed, almost closing the umbilicus. The largest specimens seen (from Dirgag) have a shell-length of 7.3 mm. but the majority of adult specimens in both of the large samples do not exceed 6.0 mm. shell-length, with maximum width 3.4 mm. and aperture length also 3.4 mm.

The anatomy of the animal is in no way exceptional. The mantle is light grey, densely spotted with black and the rest of the body is darkly pigmented so that the living snail appears black. The male copulatory organ is like that of most members of the *B. forskali* group, the sheath is a little longer and narrower than the preputium and the epiphallus is short. The radula teeth are smaller than in *B. forskali*, the cusps of the laterals are long and lanceolate and, in the majority of specimens there is an accessory cusp high up on the outer edge of the ectocones (Text-fig. 10).

The affinities of *B. beccari* have never been clear. Paladilhe recognized that it was closely related to many species characteristic of the African fauna but he was able to distinguish between it and *lamellosa* Roth and *vitrea* "Parreys", both now regarded as synonyms for *B. forskali* (Ehrenberg). Germain (1921) included *beccari* with the Mauritian species *cernicus* in the synonymy of *forskali* and Mandahl-Barth (1957), following Germain, provisionally placed *beccari* in the synonymy of *cernicus*. The general appearance of the shell of *beccari* is close to some forms of *senegalensis* from the Gambia (Wright, 1959b) but it is distinguished from that species by the presence (on most specimens) of a weak carination on the upper part of the early whorls. *B. beccari* differs from most forms of *B. forskali* in the poorly developed ribbing of even the early whorls and in its generally more obese body whorl and less exerted spire. The radula teeth are smaller than *senegalensis*, *forskali* or *scalaris* and there is no fusion of the endo- and mesocones of the laterals as in *cernicus*.

The importance of *B. beccari* as an intermediate host for *Schistosoma haematobium*



Radula teeth.

FIG. 5. *Biomphalaria rueppelli*. Central, 1, 11 and 16.

FIG. 6. *Gyraulus convexiusculus*. Central, 1 and 15.

FIG. 7. *Bulinus sericinus*. Central, 1, 6 and 12.

FIG. 8. *B. reticulatus* from Rassais. Central, 1, 2, 9 and 16.

FIG. 9. *B. reticulatus* from Kienmy. Central, 1, 2, 9 and 16.

in the coastal plain regions of Aden is described elsewhere (Wright, in press). The ability of the species to act as a host for this parasite suggests possible affinities with either *B. senegalensis* or *B. cernicus*. Ecologically *beccari* differs from *senegalensis*, a snail so far only known from temporary rain pools with a low calcium content, in that it is found in permanent, flowing water with a high calcium content.

Family *LYMNAEIDAE*

Lymnaea truncaluta (Müller)

(Pl. I, 18–20)

Buccinum truncatulum Müller 1774, vol. II, p. 130.

Lymnaea (*Galba*) *truncatula* Connolly, 1941, p. 33.

UPPER AULAQI : Tarbak, Wadi Amhadu (part of Wadi Hatib), under small stones and amongst gravel both in the water and on the edge of the stream at a point where it was flowing rapidly.

Several dozen specimens of this species were collected from a very localized and unusual habitat. The shells do not differ in any significant respect from specimens from the Ethiopian highlands (Wright & Brown, 1962) and the anatomy of the reproductive system shows no unusual characters. The radula teeth are interesting in that the first five laterals are all bicuspid, the endocone is reduced to a slight swelling on the inner edge of the mesocone and this cusp and the ectocone are unusually long and dagger-like (Text-fig. 11). The endocone appears as a discrete cusp near the tip of the mesocone in the sixth row and in the next few rows the division becomes more marked. Transition to the marginals occurs by subdivision of the endocone, the ectocone remains undivided and eventually disappears as do most of the divisions of the endocone so that the extreme marginals are bicuspid.

Connolly (1941) recorded two specimens of this species collected from a muddy brook near San'a, Yemen. The present record merely extends its known distribution a little to the south and east.

Family *ANCYLIDAE*

(Pl. II, 15–22)

Ancylus fluviatilis Müller. 1774, Vol. II, p. 201

Pseudancylus abyssinicus Connolly, 1941, p. 34.

Pseudancylus argenteus Connolly, 1941, p. 37, Pl. III, figs. 11–12.

UPPER AULAQI : Sumayfah, Wadi Yeshbum, from a deep, shaded rock-pool in a side gully near Yeshbum, about 3,200 ft.

Tarbak, Wadi Amhadu (part of Wadi Hatib), from the rocky sides of a swift-flowing, shallow channel, in the stream bed, about 4,500 ft.

There are no obvious differences between the ancyliids collected in Upper Aulaqi and European specimens of *A. fluviatilis*. The description of the genital system of this species by Lacaze-Duthiers (1899) differs only from the Aden material in that

he shows the flagellum to open into the penis sheath while in my specimens the duct appears to open separately into the preputium (Text-fig. 4); this is a character which could so easily be affected by fixation methods that it cannot be regarded as having any taxonomic importance.

Connolly (1941) described *Pseudancylus argenteus* from pools in Shab Samua, Hureidha in the Hadhramaut and recorded *P. abyssinicus* (Jickeli) from a pond near Haz in Yemen. In the collection of the British Museum (Natural History) there is a sample of *P. argenteus* (identified by Connolly) from Mesayid, Yemen. The shells of my material from Sumayfah compare well with Connolly's *abyssinicus* and the larger specimens from Tarbak are only distinguishable from Connolly's Yemen material of *argenteus* by their darker colour. The type series of *argenteus* have the apex of the shell less sharply recurved than in the other samples. Connolly noted that in *argenteus* the ectocone of the marginal radula teeth is unicuspid while in *abyssinicus* and *fluviatilis* the ectocone is subdivided. This observation was based on radula preparations made from the type series of *argenteus* and from the Yemen sample of *abyssinicus*. Re-examination of the original slides shows that this character is slightly variable. In the majority of my specimens the ectocone is unicuspid but in one radula it is undivided in the marginals on one side and bicuspid on the other (Text-fig. 12).

Attention was drawn to the similarity between the radulae of *Ancylus fluviatilis* and *abyssinicus* by Jickeli (1874) and the close relationship between the two species was emphasized by Walker (1914). When preserved material from the highlands of Ethiopia becomes available it is almost certain that the anatomical identity of *abyssinicus* with *fluviatilis* will be confirmed. The range of this Palearctic species must now be extended to include the highland areas of South-west Arabia.

Family *THIARIDAE*

Melanoides tuberculata (Müller)

(Pl. II, 23)

Nerita tuberculata Müller, 1774, Vol. II, p. 191.

Melanoides tuberculata Connolly, 1941, p. 35.

FAHDLI: Wadi Hasan at Dirgag, Abyan.

LOWER YAFAI: Nabwa spring and Wadi Bana, Bateis, Abyan.

UPPER AULAQI: As Sufal, Wadi Yeshbum and several places in the Wadi Hatib.

HAUSHABI: Wadi Tiban at Museimir.

This species is almost universal in its distribution in South-west Arabia, usually in gently flowing water. Specimens from Abyan in the coastal plain reach a greater maximum size than those from the hill regions.

DISCUSSION

All of the species in this collection have been obtained before in various parts of South-west Arabia but this is the first material which has been subjected to detailed anatomical examination to elucidate the relationships of some of the species. Thus,

Biomphalaria arabica is shown to be indistinguishable from *B. rueppelli* of Ethiopian origin, the *Bulinus truncatus* of most previous authors is more closely related to the highland species, *B. sericinus*, Connolly's *B. truncatus* var. from the Hadhramaut is the rare East African *B. reticulatus* and *Pseudancylus argenteus* and *P. abyssinicus* are only local forms of *Ancylus fluviatilis*. The specimens collected in Upper Aulaqi state are the first from that area and all thus provide new locality records which either extend or fill in gaps in known distribution patterns.

Connolly (1941) noted a marked difference between the non-marine molluscan fauna of South-west Arabia and that of Hejaz and Nejd. Mattingly and Knight (1956) found that the boundary line between the Palearctic and Ethiopian zoogeographical regions defined by Chapin (1923) on the basis of the avifauna also holds good for the mosquitoes of Arabia. This line runs roughly south-east from a point on the Red Sea coast near Jeddah to the coast of Oman opposite the Kuria Muria Islands, and, as a result, places the whole of Yemen and the Aden Protectorates in the Ethiopian region. Scott (1939) in a general account of the natural history of South-west Arabia pointed out that the major regional component of the flora and fauna of the hot valleys is African modified by an Oriental influence while in the highlands there is a well-marked Palearctic element. An analysis of the regional components of the mosquito fauna of Arabia as a whole by Mattingly and Knight showed that the bulk of the species are Palearctic but that there is a strong Ethiopian element in the South-west and the Oriental influence is small and mostly confined to the coast. These authors also concluded that the mosquito fauna of Socotra is predominantly Palearctic.

The freshwater molluscs appear to conform well to the general zoogeographical picture in South-west Arabia. Many of the older records are not sufficiently reliable for consideration but, through the kindness of Dr. Ruth Turner of the Museum of Comparative Zoology at Harvard I have been able to examine material collected by Dr. R. E. Kuntz in Yemen and identified by Dr. J. Bequaert. These specimens, in conjunction with my own and material in the collection of the British Museum (Natural History) provide a reasonable basis for discussion.

The principal influence is clearly Ethiopian and, in the highland areas, this influence can be seen in the narrow political-geographical sense rather than the broader zoogeographical meaning of the adjective. Both *Biomphalaria rueppelli* and *Bulinus sericinus* are characteristic of the highlands of Abyssinia and the relationship is further reinforced by Kuntz's specimens of *Segmentorbis angusta* (Jickeli) found near Ma'bar, Yemen. Mattingly and Knight (loc. cit.) pointed out that the number of Ethiopian species in the Arabian mosquito fauna is inclined to be exaggerated by the inclusion of forms whose distribution in the Ethiopian region is limited and which are more accurately assigned to the Palearctic. This is also the case with the freshwater mollusca in that *Lymnaea truncatula*, *Ancylus fluviatilis* and *Pisidium casertanum* are common to both the Abyssinian and South-west Arabian highlands but are, in fact widely distributed Palearctic species. Regardless of their wider distribution, the presence of these three species isolated in the highland areas on both sides of the southern Red Sea provides very strong evidence in favour of a common origin of the two faunas.

Both *Bulinus beccari* and *B. reticulatus* are obvious African elements. *B. beccari* appears to be an endemic Arabian form but more detailed investigations of the coastal regions of North-east Africa may reveal its presence there. It is very close to some forms of *B. forskali* and it has been confused with that species in the past. It is probably merely a local race of *B. forskali*, no more entitled to specific distinction than many other races, but for its obvious epidemiological importance. *B. reticulatus* presents exactly the opposite problems to those posed by *B. beccari*. It is not a well-known species and the full range of its variation has not been studied; the material from Aden differs markedly in characters of the radula and male copulatory organ from topotype specimens from Kenya and the Aden form is also a proven host for *Schistosoma haematobium* but the intermediate host potential of African *B. reticulatus* has not been investigated. In another paper (Wright, in press) I have suggested that *B. crystallinus* and *B. camerunensis* may be relicts of an ancestral bulinid stock and it is possible that *B. reticulatus* also falls into this category. If this is the case then considerable differences are to be expected between isolated populations of an ancient form and morphological differences such as those found between Arabian and Kenyan *B. reticulatus* suggest a long period of separation.

A further possible Ethiopian influence in the Arabian fauna is *Lymnaea arabica* Smith, 1894. Hubendick (1951) considers that the species is probably a local form of the extremely variable African *L. natalensis*. Specimens collected by Kuntz in Yemen were identified by Bequaert as *L. exserta*, a form of *L. natalensis* and several samples in the collection of the British Museum (Natural History) from Yemen, Western Aden Protectorate and Dhufar have been assigned to *L. caillaudi*, also a synonym of *L. natalensis*. However, Connolly (1941) recorded *L. auricularia* from near San'a, Yemen and Dr. Bequaert also identified samples collected by Kuntz from near M'bar and Dhamar as this species. Hubendick (1951) treats *L. natalensis* as the African part of the *L. auricularia* super-species which extends throughout the Palearctic and Oriental regions. However, *L. auricularia*, *L. natalensis* and some of the Oriental forms of *L. auricularia* can be distinguished from one another by the chromatographic pattern of fluorescent substances in their body-surface mucus (Wright, 1959a). Unfortunately no material belonging to this complex was found during the present survey but, if living specimens become available for study in the future, it should be possible to decide whether they are derived from Ethiopian, Palearctic or Oriental origins.

The only clearly Oriental element in the present collection is *Gyraulus convexiusculus*, a species described originally from Afghanistan but with a wide range in South-east Asia. Kuntz collected a large sample of this species near San'a, Yemen and Connolly records it from Wadi Jedd in the Hadrhamaut. Pallary (1928) reported *Indoplanorbis exustus* from Muscat and Connolly included this species in his faunal list for Southern Arabia but expressed doubts as to the correct identification of the material. However, Pallary's specimens are in the collection of the British Museum (Natural History) and I am able to confirm that they are shells of *I. exustus*. Two samples in Kuntz's Yemen collection identified as this species are in fact *Biomphalaria rueppelli* and Pallary's specimens are the only confirmed record for *I. exustus* in Southern Arabia. Muscat lies in the extreme south-eastern corner of the Arabian

peninsula on the Persian Gulf, the commonly accepted boundary between the Palearctic and the Oriental regions, and the presence of this typically Oriental species is not, therefore, surprising. A collection of freshwater gastropods from Socotra has been examined and in five large samples the dominant species present was *I. exustus*, an Oriental influence which is in contrast to Mattingly and Knight's comments on the predominantly Palearctic nature of the island's mosquito fauna. The only other species present in the Socotran collection was *Melanoides tuberculata* an almost ubiquitous prosobranch with a range extending from West Africa through to South-east Asia. In the Western Aden Protectorate this is the most abundant species of snail and, with the possible exception of *Gyraulus convexiusculus*, is the only one that occurs both in the coastal plain and in the highlands.

The conclusions reached by this examination of the relationships of the freshwater gastropods of South-west Arabia are in accordance with the general zoogeographical trends in the area. The principle influence is Ethiopian with a Palearctic component in the highlands (a component which is shared with the Ethiopian highlands) and a small Oriental element which appears to have a wide altitudinal range. Recent surveys by medical parasitologists have given the impression that the molluscan fauna of the area is of the Mediterranean type. This impression was created by the treatment of *Biomphalaria arabica* as a sub-species of the *alexandrina* group rather than as a member of the *pfeifferi* complex, by the failure to recognize the differences between the highland *Bulinus sericinus* and the lowland *B. truncatus* and by the automatic inclusion of *B. beccari* in the synonymy of *B. forskali*. That these apparently academic points have an epidemiological significance is shown by the failure of attempts to infect Middle Eastern strains of *B. truncatus* with two strains of *Schistosoma haematobium* from the Western Aden Protectorate (Wright, in press). They explain also Witenberg and Saliternik's (1957) failure to infect Israeli *B. truncatus* with *S. haematobium* obtained from Yemeni immigrants.

SUMMARY

Anatomical study of a small collection of freshwater gastropods from the Western Aden Protectorate has permitted a reassessment of the affinities of some of the species recorded from South-west Arabia. The species represented in the collection are *Biomphalaria rueppelli*, *Gyraulus convexiusculus*, *Bulinus sericinus*, *B. reticulatus*, *B. beccari*, *Lymnaea truncatula*, *Ancylus fluviatilis* and *Melanoides tuberculata*. The zoogeographical aspects of the basommatophoran fauna are discussed and the epidemiological significance of the bulinids as intermediate hosts for human blood-flukes is mentioned.

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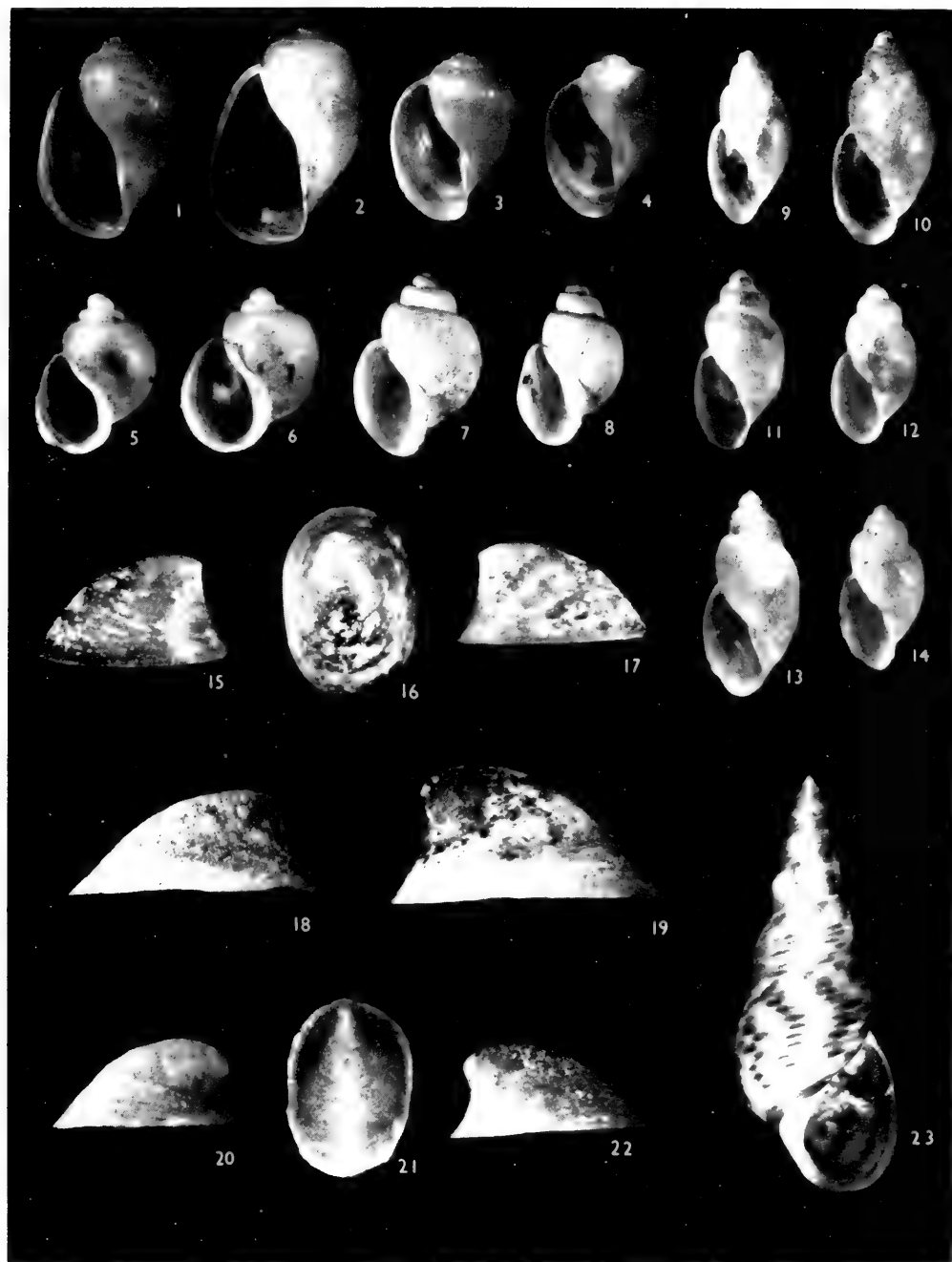
PLATE I

- FIGS. 1-3. *Biomphalaria rueppelli*. Holotype of *Planorbis arabica*.
FIGS. 4-6. *B. rueppelli*. Sumayfah, Upper Aulaqi.
FIGS. 7-8. *B. rueppelli*. Tarbak, Upper Aulaqi.
FIGS. 9-14. *Gyraulus convexiusculus*. Tarbak, Upper Aulaqi.
FIGS. 15-17. *G. convexiusculus*. Kandahar, Afghanistan.
FIGS. 18-20. *Lymnaea truncatula*. Tarback, Upper Aulaqi.
(All figures $\times 4$.)



PLATE

- FIGS. 1-4. *Bulinus sericinus*. Tarbak, Upper Aulaqi.
FIGS. 5 and 6. *B. reticulatus*. Rassais, Upper Aulaqi.
FIGS. 7 and 8. *B. reticulatus*. Marbum, Upper Aullqi.
FIGS. 9 and 10. *B. beccari*. Bateis, Abyan, Lower Yafai.
FIGS. 11-14. *B. beccari*. Dirgag, Abyan, Fahdli.
FIGS. 15-17. *Ancylus fluviatilis*. Holotype of *Pseudancylus argenteus*.
FIGS. 18 and 19. *A. fluviatilis*. Tarbak, Upper Aulaqi.
FIGS. 20-22. *A. fluviatilis*. Sumayfah, Upper Aulaqi.
FIG. 23. *Melanoides tuberculata*. Musemir, Haushabi.
(All figures $\times 4$.)



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OBSERVATIONS ON THE
CHAETOTAXY OF THE LEGS IN
THE FREE-LIVING GAMASINA
(ACARI : MESOSTIGMATA)

G. OWEN EVANS



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Department of Zoology, British Museum (Natural History)



Pp. 275-303 ; 15 Text-figures

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SYNOPSIS

Studies on the chaetotaxy of the legs of the free-living Gamasina have shown that segmental chaetotactic patterns provide valuable taxonomic criteria for the classification of the group. The application of leg chaetotaxy to the classification of the Gamasina at species, genus and family levels is discussed. A system of setal nomenclature is introduced for individual leg segments.

INTRODUCTION

During the last ten years, studies on the chaetotaxy of the idiosoma and the gnathosoma of the Mesostigmata have resulted in the introduction of many new taxonomic criteria for the classification of the group. These studies are now extended to the ambulatory appendages which have been largely ignored in both descriptive and classificatory works on the Mesostigmata.

The present contribution is restricted to an account of the leg chaetotaxy in the free-living Gamasina. My studies are as yet incomplete, particularly as regards the ontogenetic development of the chaetotaxy, but they do indicate that leg chaetotaxy can provide taxonomic characters of comparable value to those based on the chaetotaxy of the gnathosoma and idiosoma. It is hoped that this paper will stimulate other acarologists to investigate further this interesting aspect of the morphology of the Mesostigmata.

TERMINOLOGY

For the purpose of setal nomenclature, each segment of the legs is considered to have four setae-bearing surfaces, namely, a dorsal (*d*), a ventral (*v*), an antero-lateral (*al*) and a postero-lateral (*pl*). The anterior and posterior faces of the segment (or leg) refer to the positions adopted when the leg is extended laterally, that is, at right angles to the longitudinal axis of the idiosoma. The setae on the dorsal and ventral

surfaces of a segment are divided into an anterior and a posterior series according to their positions relative to the anterior and posterior faces of the segment. The setae are numbered from the distal to the proximal end of the segment. When the distribution of the setae is such that their division into an anterior and posterior series is not possible, they are simply referred to as dorsal (*d*) and ventral (*v*) setae. The unpaired setae which appear during ontogeny on the dorsal and ventral surfaces of tarsi II–III are termed medio-dorsal (*md*) and medio-ventral (*mv*), respectively. The chaetotaxy of tarsus I is not considered in the present study.

It is often necessary to refer to the number of setae on a particular segment of the leg in the course of descriptive work. A reference to the total number of setae is of limited value since it gives no indication of the distribution of the setae on a segment. Considerably more information is given when the numerical data are divided into four sections to coincide with the four setae-bearing faces of the segment. Thus, the data may be expressed as follows:

$$(\text{antero-laterals} \left/ \frac{\text{dorsals}}{\text{ventrals}} \right/ \text{postero-laterals}).$$

Each segmental formula is accompanied by a specific reference to the segment and to the postembryonic developmental stage to which the data apply. For example, Femur I, L ($2 \left/ \frac{4}{2} \right/ 2$) implies that the femoral segment of leg I in the larva bears two antero-laterals, four dorsals, two ventrals and two postero-laterals. The abbreviations L, P, D, A (σ or φ) are used, respectively, for larva, protonymph, deutonymph and adult (male and female). This type of segmental formula has been found to be adequate for representing the chaetotactic data of the trochanter and femur but not of the genu and tibia. In many instances, it has been found that the total number of setae on the dorsal and ventral surfaces of the genu and tibia may be the same in widely separated groups of species although the actual chaetotactic patterns of these segments may be quite different owing to differences in the numbers of setae in the anterior and posterior series of the dorsal and/or ventral surfaces of the segments. These differences in chaetotactic patterns may be shown numerically by extending the above chaetotactic formula to include the number of setae in the anterior and posterior series of the dorsal and ventral surfaces, thus,

$$(\text{antero-laterals} \left/ \frac{\text{antero-dorsals}}{\text{antero-ventrals}}, \frac{\text{postero-dorsals}}{\text{postero-ventrals}} \right/ \text{postero-laterals}).$$

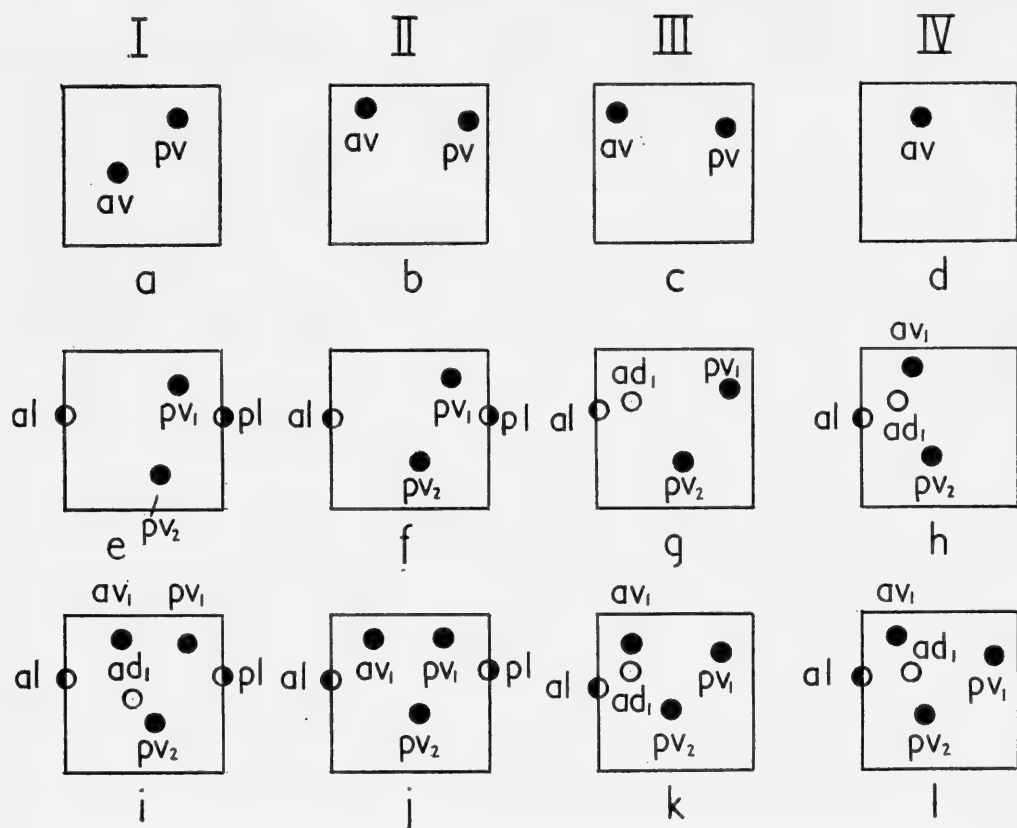
This formula is used for the chaetotaxy of the genua and tibiae throughout this paper.

In the diagrammatic representation of segmental chaetotaxy, the open circles (○) refer to dorsal setae, the black dots (●) to ventral setae and the half-open circles (◐) to lateral setae.

THE ONTOGENETIC DEVELOPMENT OF THE CHAETOTAXY OF THE LEGS IN *PERGAMASUS* (PARASITIDAE)

The following account of the development of the leg chaetotaxy in the larval and protonymphal stages of *Pergamasus* applies to the majority of the free-living Gama-

sina I have examined. The adult chaetotaxy which is determined at the deutonymphal stage is considerably more variable.



FIGS. 1a-l. Diagrammatic representations of the chaetotaxy of the coxae and trochanters of legs I-IV in *Pergamasus* (Parasitidae). a-d, chaetotaxy of the coxae of legs I-IV. e-h, chaetotaxy of the trochanters of legs I-IV in the larva and protonymph. i-l, chaetotaxy of trochanters I-IV in the deutonymph and adult.

ad, antero-dorsal seta; al, antero-lateral seta; av, antero-ventral seta; pd, postero-dorsal seta; pl, postero-lateral seta; pv, postero-ventral seta; I-IV, legs I-IV.

Coxae I-IV (Text-figs. 1a-d)

The chaetotaxy of coxae I-III is determined at the larval stage; each segment bearing two ventral setae (av and pv). There is a remarkable constancy in the relative positions of the setae. Coxa IV bears a single ventral seta in the protonymph and in the succeeding developmental stages. This seta is possibly homologous to seta av of coxae II and III but has moved to a median position on the segment. The migration of a seta to a median position on the dorsal, ventral and lateral surfaces of a segment when the corresponding member of the pair is missing, is a common feature of segmental chaetotaxy.

Trochanters I-IV (Text-figs. 1e-l)

Trochanter I has four setae in the larva and protonymph, comprising two laterals (*al* and *pl*) and two ventrals (*pv*₁ and *pv*₂). Two setae are added to the segment in the deutonymph, one dorsal (*d*) and one ventral (*av*). This chaetotaxy is retained by the adult. The chaetotaxy of trochanter II in the larva and protonymph is similar to that of trochanter I at those stages but in the deutonymph only one seta (*av*) is added to the segment. Four setae occur on trochanter III in the larva and on trochanters III and IV in the protonymph, and five setae on each of these segments in the deutonymph and adult. The distribution of these setae is more variable than the setae of trochanters I and II. This is probably due to the asymmetrical development of the trochanters (and femora) of legs III and IV as the result of the posterior direction of legs III and IV.

Femora I-IV (Text-figs. 2a-i)

Femora I and II have a completely different chaetotaxy from femora III and IV as regards the number and the distribution of the setae.

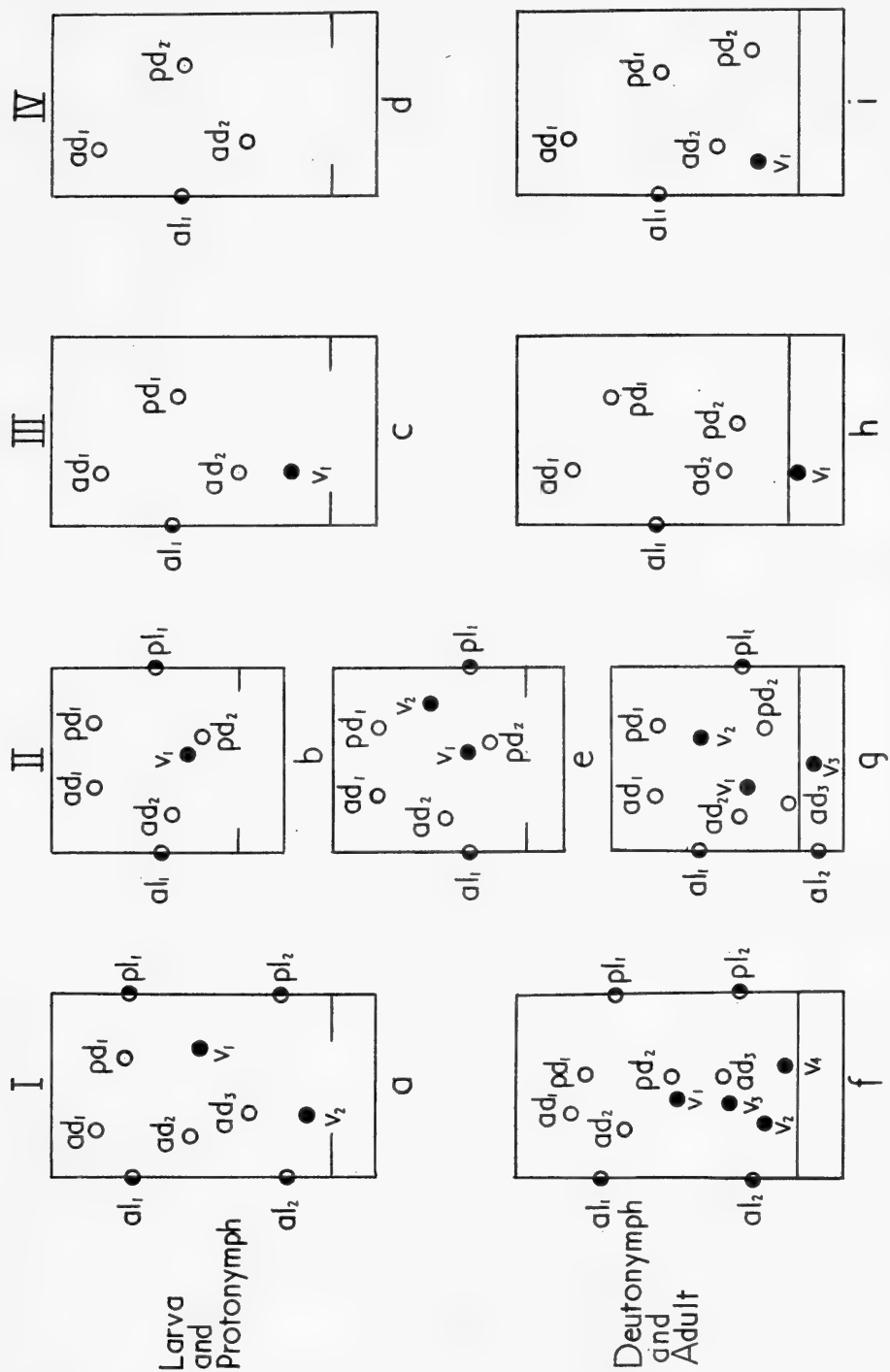
Femur I in the larval and protonymphal stages bears ten setae—four dorsals (*ad*₁, *ad*₂, *ad*₃ and *pd*₁), four laterals (*al*₁, *al*₂, *pl*₁ and *pl*₂) and two ventrals (*v*₁ and *v*₂). The deutonymphal complement of thirteen setae is formed by the addition of one dorsal (*pd*₂) and two ventrals (*v*₃ and *v*₄). This number is retained by the adult. There are no setae situated proximal of the lyriform fissure. Setae *pd*₂ and *ad*₃ assume a median position on the dorsal surface of the segment.

Femur II in the larva (Text-fig. 2b) has seven setae (*ad*₁, *ad*₂, *pd*₁, *pd*₂, *v*₁, *al*₁ and *pl*₁). In the protonymph (Text-fig. 2e) a single ventral seta (*v*₂) is added to the segment whilst in the deutonymph (Text-fig. 2g) three setae appear, one lateral (*al*₂), one dorsal (*ad*₃) and one ventral (*v*₃). Setae *al*₂ and *v*₃ are situated proximal to the lyriform fissure. The chaetotaxy of the female resembles that of the deutonymph but in the male the segment becomes swollen and seta *v*₁ and often *v*₂ hypertrophy and form spur-like structures. The main femoral spur develops from seta *v*₁ and the axillary spur from seta *v*₂. Seta *v*₃ in the male moves to a more distal position and never lies proximal to the lyriform fissure.

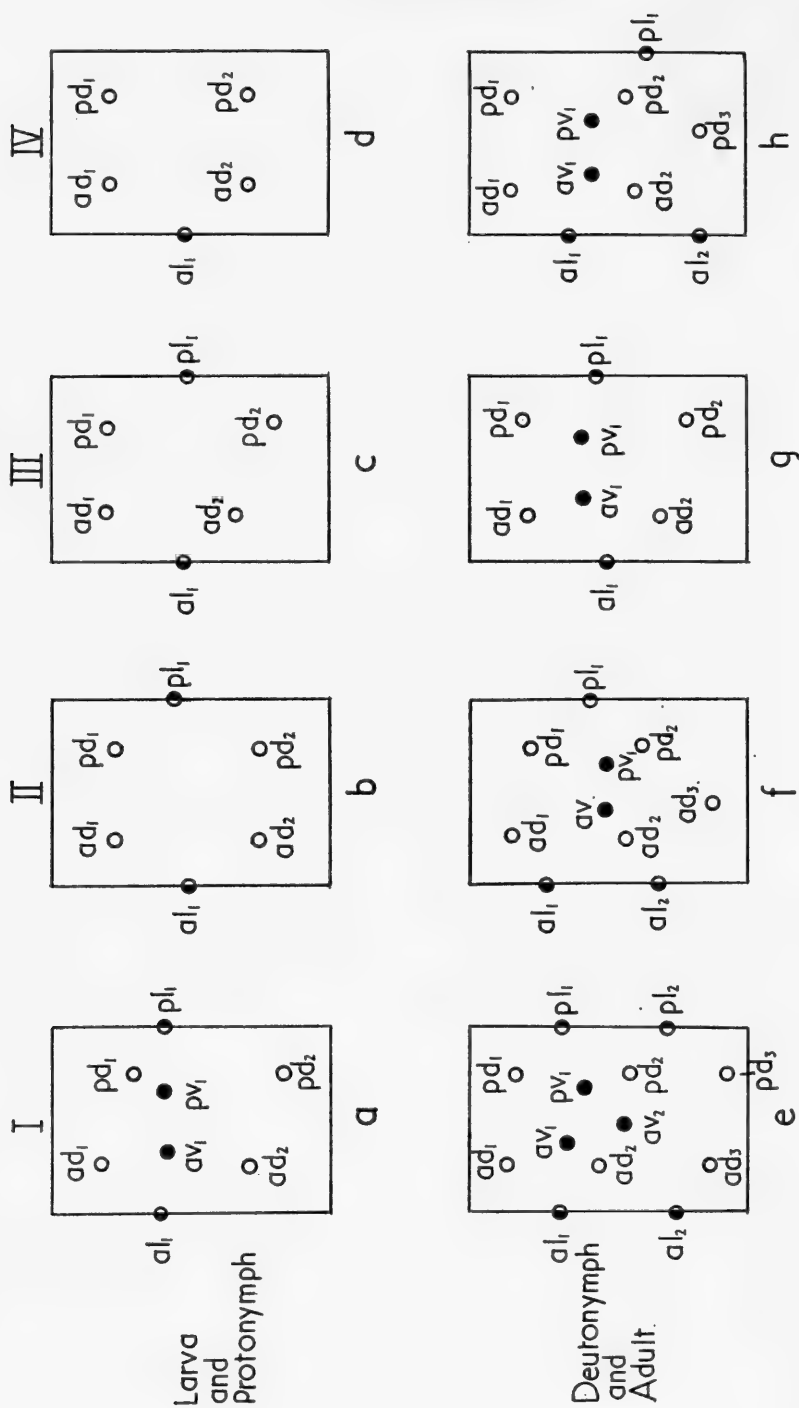
Femur III in the larva and protonymph carries five setae, comprising three dorsals (*ad*₁, *ad*₂ and *pd*₁), one lateral (*al*) and one ventral (*v*). Only one seta (*pd*₂) is added to the segment in the deutonymph. The chaetotaxy of femur IV in the protonymph resembles that of femur III at that stage except for the absence of the ventral seta (*v*) which appears with *pd*₂ in the deutonymph. The deutonymphal chaetotaxy of femora III and IV is retained by the adult.

Genua I-IV (3a-h)

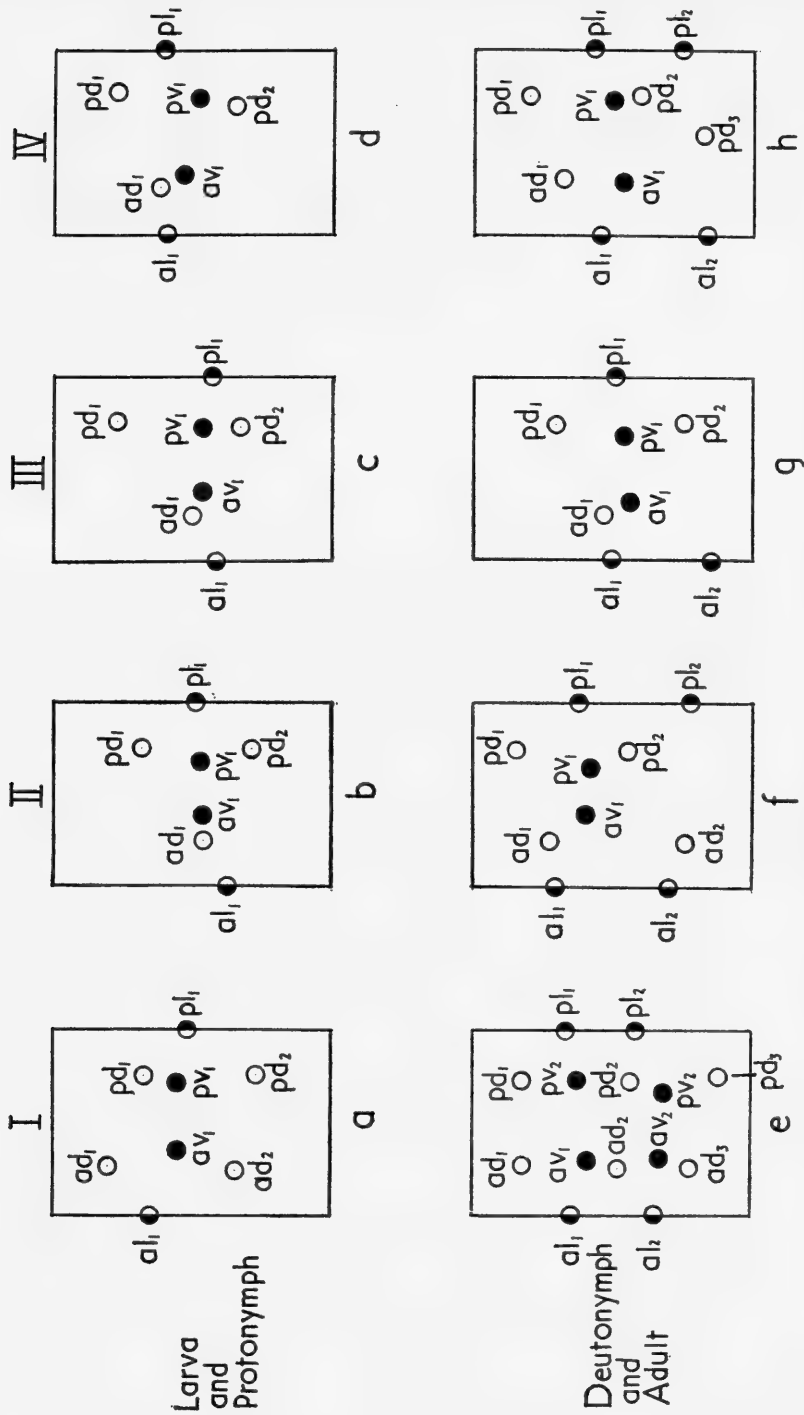
Genu I carries eight setae in the larva and protonymph—four dorsals (*ad*₁, *ad*₂, *pd*₁, *pd*₂), two laterals (*al*₁ and *pl*₁) and two ventrals (*av*₁ and *pv*₁). This number is increased to thirteen in the deutonymph by the appearance of one ventral (*av*₂), two laterals (*al*₂ and *pl*₂) and two dorsals (*ad*₃ and *pd*₃). Seta *av*₂ migrates medially so that the three ventral setae form an inverted triangle. Six setae occur on genu II



FIGS. 2a-i. Diagrammatic representations of the chaetotaxy of the femora of legs I-IV in the larva, protonymph, deutonymph and adult of *Pergamasus*. Abbreviations as in Fig. 1.



FIGS. 3a-h. Diagrammatic representations of the chaetotaxy of the genera of legs I-IV in the larva, protonymph, deutonymph and adult of *Pergamasus*. Abbreviations as in Fig. 1.



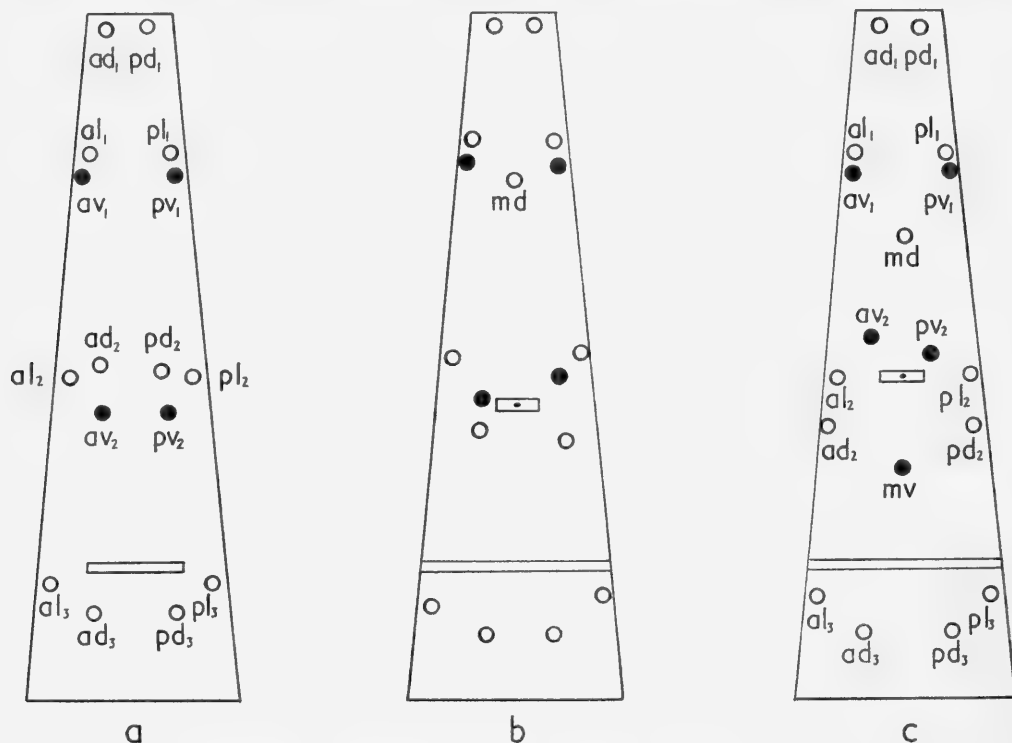
FIGS. 4a-h. Diagrammatic representations of the chaetotaxy of the tibiae of legs I-IV in the larva, protonymph, deutonymph and adult of *Pergamasus*. Abbreviations as in Fig. 1.

in the larva and protonymph comprising ad_1 , ad_2 , pd_1 , pd_2 , al_1 and pl_1 . There are no ventral setae. Five setae appear in the deutonymph, one dorsal (ad_3), two lateral (al_2 and pl_2) and two ventral (av_1 and pv_1). The chaetotaxy of genu III in the larva and protonymph is similar to that of genu II at those stages but only two setae, the ventrals av_1 and pv_1 , are added in the deutonymph. Genu IV bears five setae (ad_1 , ad_2 , pd_1 , pd_2 and al_1) in the larva and protonymph. The deutonymph adds five setae (av_1 , pv_1 , al_2 , pl_1 and pd_3).

The deutonymphal chaetotaxy of the genera is retained by the adult. In the males seta av_1 hypertrophies and takes the form of a spur-like structure.

Tibiae I-IV (Text-figs. 4a-h)

Tibia I in the larva and protonymph bears eight setae (ad_1 , ad_2 , pd_1 , pd_2 , al_1 , pl_1 , av_1 and pv_1). Six setae are added proximally in the deutonymph. These comprise two dorsals (ad_3 and pd_3), two laterals (al_2 and pl_2) and two ventrals (av_2 and pv_2). The deutonymphal complement of setae is retained by the adult. The tibiae of legs II and III in the larva and protonymph bear seven setae. Their chaetotaxy resembles that of tibia I in these stages except for the absence of ad_2 and the migration of ad_1 to a median position on the segment. Tibia II in the deutonymph shows an



FIGS. 5a-c. Diagrammatic representations of the chaetotaxy of tarsi II-IV in the larva (a), the protonymph (b) and the deutonymph (c) of *Pergamasus*.

md, medio-dorsal seta; *mv*, medio-ventral seta. Other abbreviations as in Fig. 1.

increase of three setae—a dorsal (ad_2) and two laterals (al_2 and pl_2). Only one seta (al_2) is added to tibia III in the deutonymph. The chaetotaxy of tibia IV in the protonymph is similar to that of tibiae II and III at that developmental stage. In comparison with tibia III, however, three setae appear on the segment in the deutonymph (setae al_2 , pd_3 and pl_2). In the male seta av_1 may hypertrophy and form a spur-like structure.

Tarsi II-IV (Text-figs. 5a-e)

The chaetotaxy of tarsi II and III in the larva consists of sixteen setae—three pairs of dorsals, three pairs of laterals and two pairs of ventrals. In the protonymph an unpaired seta (md) is added in the distal half of each of tarsi II-IV and a further unpaired seta (mv) appears ventrally in the proximal half in the deutonymph making a total of eighteen setae. This number is retained by the adult.

The chaetotactic formulae for the trochanters, femora, genua and tibiae of legs I-IV in the adults and immature stages of *Pergamasus* are as follows :

Trochanter

L, P, I ($1-\frac{0}{2}-1$), II ($1-\frac{0}{2}-1$), III ($1-\frac{1}{2}-0$), P, IV ($1-\frac{1}{2}-0$).
D, A, I ($1-\frac{1}{3}-1$), II ($1-\frac{0}{3}-1$), III ($1-\frac{1}{3}-0$), IV ($1-\frac{1}{3}-0$).

Femur

L, I ($2-\frac{4}{2}-2$), II ($1-\frac{4}{1}-1$), III ($1-\frac{3}{1}-0$).
P, I ($2-\frac{4}{2}-2$), II ($1-\frac{4}{2}-1$), III ($1-\frac{3}{1}-0$), IV ($1-\frac{3}{0}-0$).
D, A, I ($2-\frac{5}{4}-2$), II ($2-\frac{5}{3}-1$), III ($1-\frac{4}{1}-0$), IV ($1-\frac{4}{1}-0$).

Genu

L, P, I ($1-\frac{2}{1}, \frac{2}{1}-1$), II ($1-\frac{2}{0}, \frac{2}{0}-1$), III ($1-\frac{2}{0}, \frac{2}{0}-1$), P, IV ($1-\frac{2}{0}, \frac{2}{0}-0$).
D, A, I ($2-\frac{3}{2}, \frac{3}{1}-2$), II ($2-\frac{3}{1}, \frac{2}{1}-2$), III ($1-\frac{2}{1}, \frac{2}{1}-1$), IV ($2-\frac{2}{1}, \frac{3}{1}-1$).

Tibia

L, P, I ($1-\frac{2}{1}, \frac{2}{1}-1$), II ($1-\frac{1}{1}, \frac{2}{1}-1$), III ($1-\frac{1}{1}, \frac{2}{1}-1$), P, IV ($1-\frac{1}{1}, \frac{2}{1}-1$).
D, A, I ($2-\frac{3}{2}, \frac{3}{2}-2$), II ($2-\frac{2}{1}, \frac{2}{1}-2$), III ($2-\frac{1}{1}, \frac{2}{1}-1$), IV ($2-\frac{1}{1}, \frac{3}{1}-2$).

CHAETOTAXY OF THE LEGS IN THE ADULTS OF THE FREE-LIVING GAMASINA

Coxae I-IV

The chaetotaxy of the coxae is constant in the free-living Gamasina ; the details given for the developmental stages of *Pergamasus* (p. 279) applying throughout the group. The form of the coxal setae varies considerably. In *Scarabaspis* (Eviphididae), for example, both setae of coxa I and seta pv of coxa II take the form of sclerotized oval protuberances.

Trochanters I-IV

Trochanter I in the majority of the species I have examined bears six setae—two laterals (*al* and *pl*), three ventrals (*av*, *pv*₁, *pv*₂) and one dorsal (*d*). The Microsejidae, however, retain the larval complement of four setae in the adult, and in the families Macrochelidae and Phytoseiidae (with few exceptions) and the genus *Thinoseius* (Eviphididae) there are only five setae on this segment; the dorsal seta (*d*) being absent. The relative positions of the setae are remarkably constant.

The chaetotaxy of trochanter II is essentially the same in all the species investigated and comprises five setae (*al*, *av*₁, *pv*₁, *pv*₂ and *pl*). With the exception of *Microgynium* (Microsejidae), the occurrence of five setae on trochanters III and IV is also constant although the distribution of the setae on the segments is variable. In *Microgynium*, trochanter III has only four setae, thus retaining the larval pattern.

The setae on the trochanters appear to be concentrated towards the external face of the segment when the legs are in the normal position for ambulation, that is, on the posterior surfaces of trochanters I and II and the anterior surfaces of trochanters III and IV.

Femur I

Four types of chaetotaxy of femur I have been observed:

X-type ($2-\frac{4}{3}-1$).

The chaetotaxy comprises setae *al*₁, *al*₂, *ad*₁, *ad*₂, *pd*₁, *pd*₂, *pl*₁, *v*₁, *v*₂ and *v*₃ (Text-fig. 6a). The three ventral setae form an inverted triangle. I have observed this chaetotactic pattern only in the Microsejidae (*Microsejus* and *Microgynium*).

XI-type ($2-\frac{5}{2}-2$).

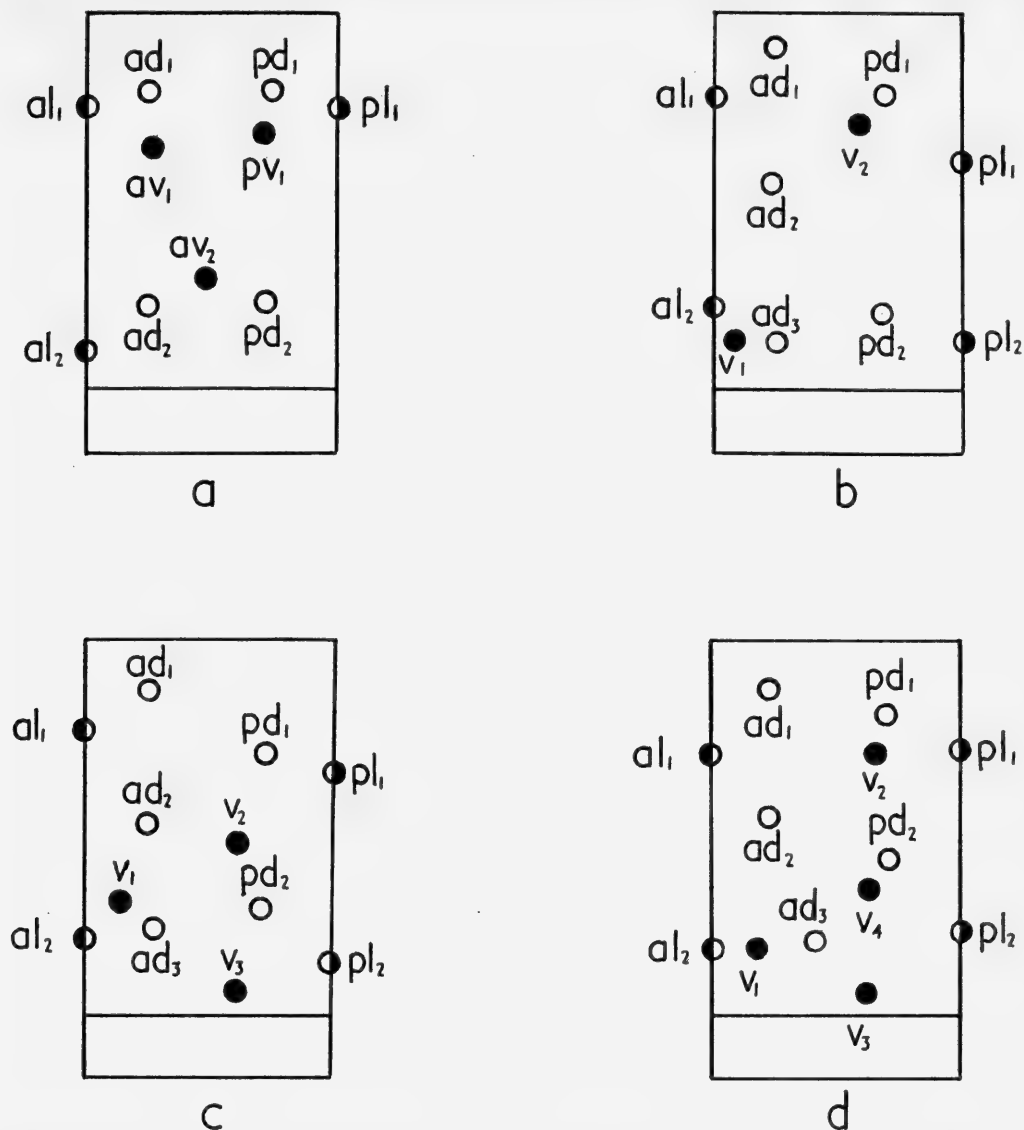
The following setae are present: *al*₁, *al*₂, *ad*₁, *ad*₂, *ad*₃, *pd*₁, *pd*₂, *pl*₁, *pl*₂, *v*₁ and *v*₂ (Text-fig. 6b). This type occurs in the genera *Sejus*, *Platyseius* and *Plesiosejus* (Aceosejidae) and *Thinoseius* (Eviphididae).

XII-type ($2-\frac{5}{3}-2$).

Seta *v*₃ is added to those occurring in the XI-type making three ventral setae (Text-fig. 6c). This chaetotaxy occurs in the families Phytoseiidae and Ameroseiidae, and in the genera *Asca* and *Halolaelaps* (Rhodacaridae) and the genera *Lasioseius*, *Proctolaelaps*, *Melichares*, *Leioseius*, *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae).

XIII-type ($2-\frac{5}{4}-2$).

This type is characterized by having four ventral setae (Text-fig. 6d). It is the most widely distributed chaetotactic pattern in the suborder and has been observed in the families Parasitidae, Veigaiaidae, Arctacaridae, Laelaptidae, Zerconidae, Epicriidae, Macrochelidae and Pachylaelaptidae, and in the genera *Eviphis*, *Alliphis*, *Pelethiphis* and *Scarabaspis* (Eviphididae), and *Rhodacarus*, *Rhodacarellus*, *Euryparasitus*, *Gamasellus*, *Ologamasus* and *Gamasiphis* (Rhodacaridae).



FIGS. 6a-d. Diagrammatic representation of the chaetotaxy of femur I in the free-living Gamasina, *a*, **X-type** (Microsejidae). *b*, **XI-type** (Aceosejidae). *c*, **XII-type** (Ameroseiidae). *d*, **XIII-type** (Eviphididae).

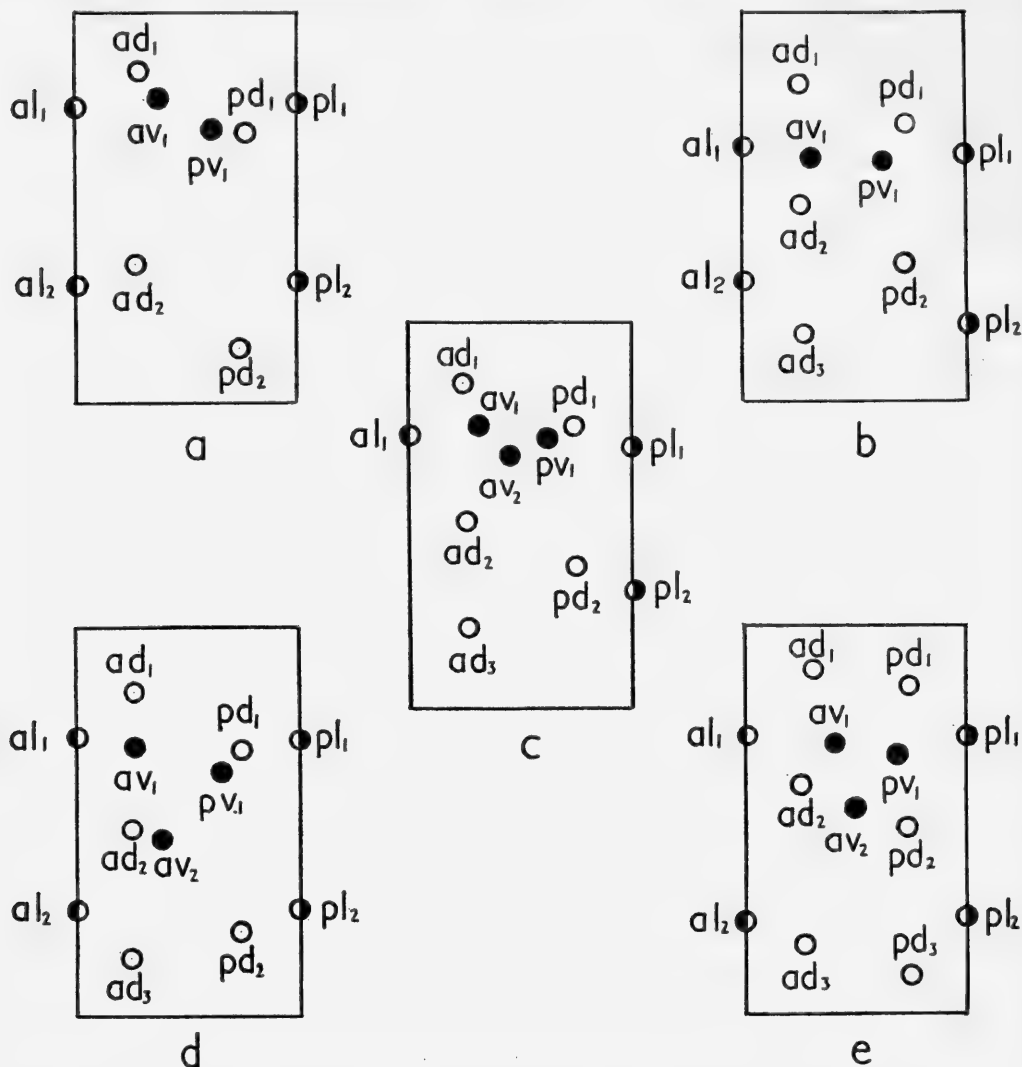
Abbreviations as in Fig. 1.

Genu I

I have observed five types of chaetotactic patterns of genu I; the number of setae ranging from ten to thirteen.

X-type ($2-\frac{2}{1}, \frac{2}{1}-2$).

The following setae are present : $ad_1, ad_2, pd_1, pd_2, av_1, pv_1, al_1, al_2, pl_1, pl_2$ (Text-fig. 7a). This type is characteristic of members of the families Phytoseiidae and Microsejidae.



FIGS. 7a-e. Diagrammatic representations of the chaetotaxy of genus I in the free-living Gamasina. a, **X-type** (Phytoseiidae). b, **XIb-type** (Macrochelidae). c, **XIa-type** (Evi-phididae). d, **XII-type** (Aceosejidae). e, **XIII-type** (Parasitidae).

Abbreviations as in Fig. 1.

XIa-type ($1-\frac{3}{2}, \frac{2}{1}-2$).

This chaetotactic pattern differs from all others on genus I in having a single

antero-lateral (al_1) seta. The setal complement is $al_1, ad_1, ad_2, ad_3, pd_1, pd_2, pl_1, pl_2, av_1, av_2$ and pv_1 (Text-fig. 7c). I have only observed this pattern in the Eviphididae.

XIb-type ($2-\frac{3}{1}, \frac{2}{1}-2$).

This differs from the X-type in having an additional dorsal seta, ad_3 (Text-fig. 7b). It is characteristic of the Macrochelidae.

XII-type ($2-\frac{3}{2}, \frac{2}{1}-2$).

This chaetotactic pattern is similar to XIb except for the presence of an additional ventral seta (av_2). The three ventral setae form an inverted triangle owing to the migration of seta av_2 to a median position on the segment (Text-fig. 7d). It is found in the Ameroseiidae and in the genera *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae), *Asca*, *Digamasellus* and *Halolaelaps* (Rhodacaridae) and *Pachyseius* (Pachylaelaptidae).

XIII-type ($2-\frac{3}{2}, \frac{3}{1}-2$).

The XIII-type is characterized by having six dorsal (ad_1 - ad_3 and pd_1 - pd_3), in addition to two antero-laterals, two postero-laterals and three ventrals (Text-fig. 7e). I have observed this genual pattern in the families Parasitidae, Veigaiidae, Arctacaridae, Laelaptidae, Zerconidae and Epicriidae, and in the genera *Lasioseius*, *Proctolaelaps*, *Melichares*, *Leioseius*, *Sejus*, *Platyseius* and *Plesioseius* (Aceosejidae), *Pachylaelaps* and *Olopachys* (Pachylaelaptidae) and *Rhodacarus*, *Rhodacarellus*, *Euryparasitus*, *Gamasellus*, *Ologamasus* and *Gamasiphis* (Rhodacaridae).

Tibia I

The X-XIII-types of chaetotaxy observed on genu I also occur on tibia I as well as a XIV-type characterized by having four ventral setae.

X-type ($2-\frac{2}{1}, \frac{2}{1}-2$).

This type (Text-fig. 8a) is found in the families Phytoseiidae and Microsejidae.

XI-type ($1-\frac{3}{2}, \frac{2}{1}-2$).

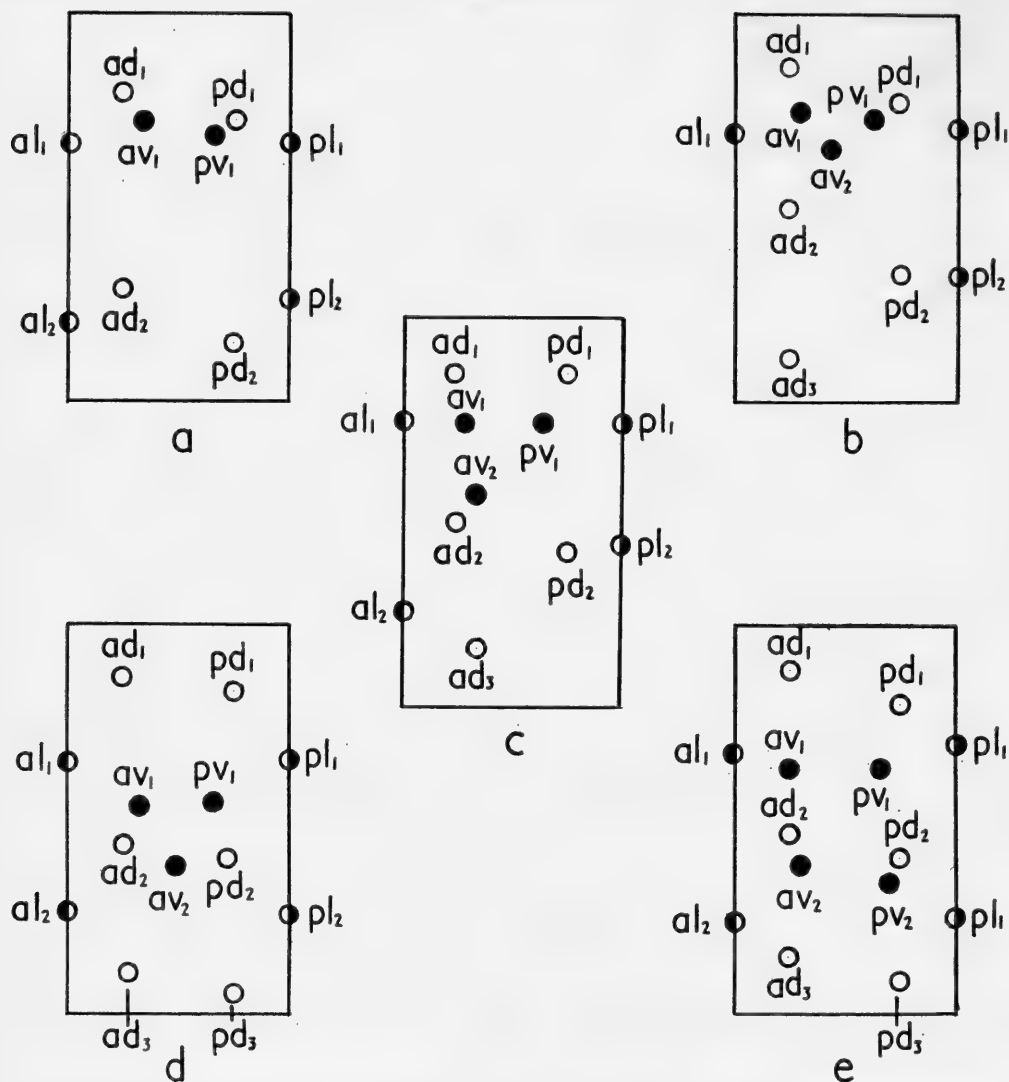
Only the XIa-type of chaetotaxy of genu I occurs on the tibia and as in the case of the genu it appears to be restricted to members of the family Eviphididae (Text-fig. 8b).

XII-type ($2-\frac{3}{2}, \frac{2}{1}-2$).

This type (Text-fig. 8c) occurs in the families Macrochelidae, Pachylaelaptidae and Ameroseiidae, and in the genera *Arctoseius*, *Iphidozercon*, *Zerconopsis* and *Plesioseius* (Aceosejidae), and *Digamasellus* and *Halolaelaps* (Rhodacaridae).

XIII-type ($2-\frac{3}{2}, \frac{3}{1}-2$).

I have observed this chaetotactic pattern (Text-fig. 8d) in the free-living Laelaptidae and in the genera *Lasioseius*, *Proctolaelaps*, *Melichares*, *Leioseius*, *Sejus*, *Platyseius* and *Plesioseius* (Aceosejidae), and *Asca* (Rhodacaridae).

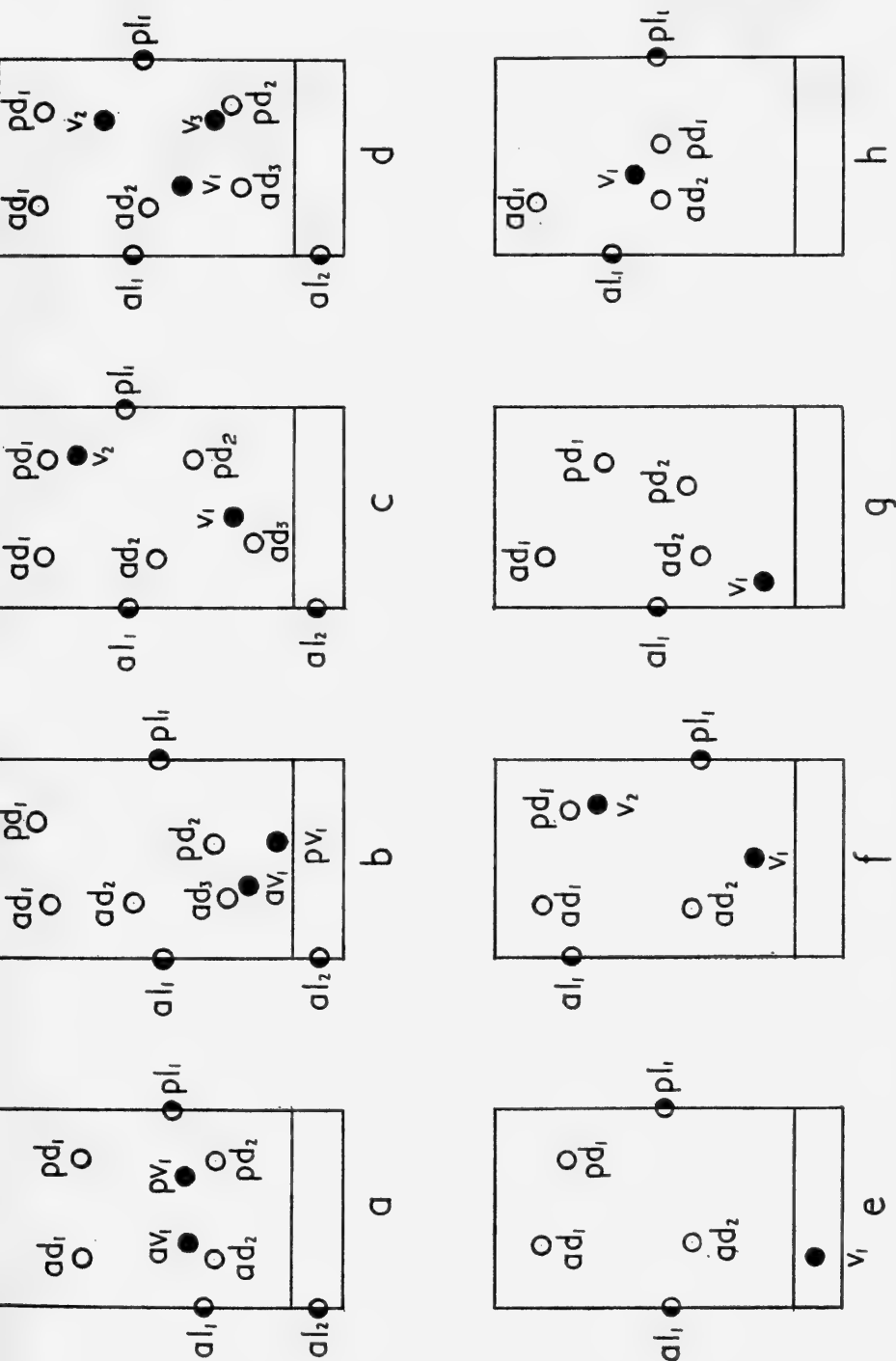


FIGS. 8a-e. Diagrammatic representations of the chaetotaxy of tibia I in the free-living Gamasina. a, **X-type** (Phytoseiidae). b, **XI-type** (Eviphididae). c, **XII-type** (Acoesejidae). d, **XIII-type** (Acoesejidae). e, **XIV-type** (Parasitidae).

Abbreviations as in Fig. 1.

XIV-type ($2-\frac{3}{2}, \frac{3}{2}-2$).

The four ventral setae arranged in the form of a rectangle readily distinguishes this pattern from the others found on tibia I (Text-fig. 8e). It occurs in the families Parasitidae, Veigaiaidae, Arctacaridae, Zerconidae, Epicriidae and in the genera *Rhodacarus*, *Rhodacarellus*, *Cyrtolaelaps*, *Euryparasitus*, *Gamasellus*, *Ologamasus* and *Gamasiphis* (Rhodacaridae).



FIGS. 9a-h. Diagrammatic representations of the chaetotaxy of femora II-IV in the free-living Gamasina. a, Femur II, **IX-type** (Microsejidae). b, Femur II, **Xb-type** (Phytoseiidae). c, Femur II, **Xb-type** (*Thinosseus*; Eviphididae). d, Femur II, **XI-type** (Laelaptidae). e, Femur III, **VI-type** (Parasitidae). f, Femur III, **VII-type** (*Thinosseus*; Eviphididae). g, Femur IV, **VI-type** (Parasitidae). h, Femur IV, **VI-type** (Plesiosejidae; Aceosejidae).

Abbreviations as in Fig. 1.

Femur II

The following four types of chaetotactic pattern have been observed on this segment :

IX-type ($2 - \frac{4}{2} - 1$).

This type has the following chaetotaxy ; al_1 , al_2 , ad_1 , ad_2 , pd_1 , pd_2 , pl_1 , av_1 and pv_1 (Text-fig. 9a). It occurs in the Microsejidae.

Xa-type ($2 - \frac{4}{3} - 1$).

The chaetotaxy comprises ad_1 , ad_2 , pd_1 , pd_2 , al_1 , al_2 , pl_1 , v_1 , v_2 and v_3 . This type has been found in the family Ameroseiidae.

Xb-type ($2 - \frac{5}{2} - 1$).

The chaetotaxy differs from the Xa-type in the presence of five dorsal setae (ad_3 additional) but only two ventral setae. It is characteristic of the Phytoseiidae, the genera *Sejus*, *Platyseius* and *Plesiosejus* (Aceosejidae), and also occurs in the genus *Thinoseius* (Eviphididae). In the latter, the ventral setae are widely separated so that one occurs in the proximal and the other in the distal half of the segment (Text-fig. 9c). In the Phytoseiidae, however, both ventral setae are usually situated in the proximal half of the segment (Text-fig. 9b).

XI-type ($2 - \frac{5}{3} - 1$).

This type has five dorsal setae and three ventrals in addition to the two antero-laterals and one postero-lateral (Text-fig. 9d). It is the most widely distributed chaetotactic pattern of femur II in the Gamasina and has been observed in the families Parasitidae, Veigaiidae, Arctacaridae, Rhodacaridae, Zerconidae, Epicriidae, Laelaptidae, Macrochelidae, Pachylaelaptidae, Aceosejidae (with the exception of *Sejus*, *Platyseius* and *Plesiosejus*) and Eviphididae (excluding *Thinoseius*).

Seta al_2 is always situated proximal to the lyriform fissure in all four types of chaetotaxy.

Genu II

Genu II carries seven, nine, ten or eleven setae.

VII-type ($2 - \frac{2}{0}, \frac{2}{0} - 1$).

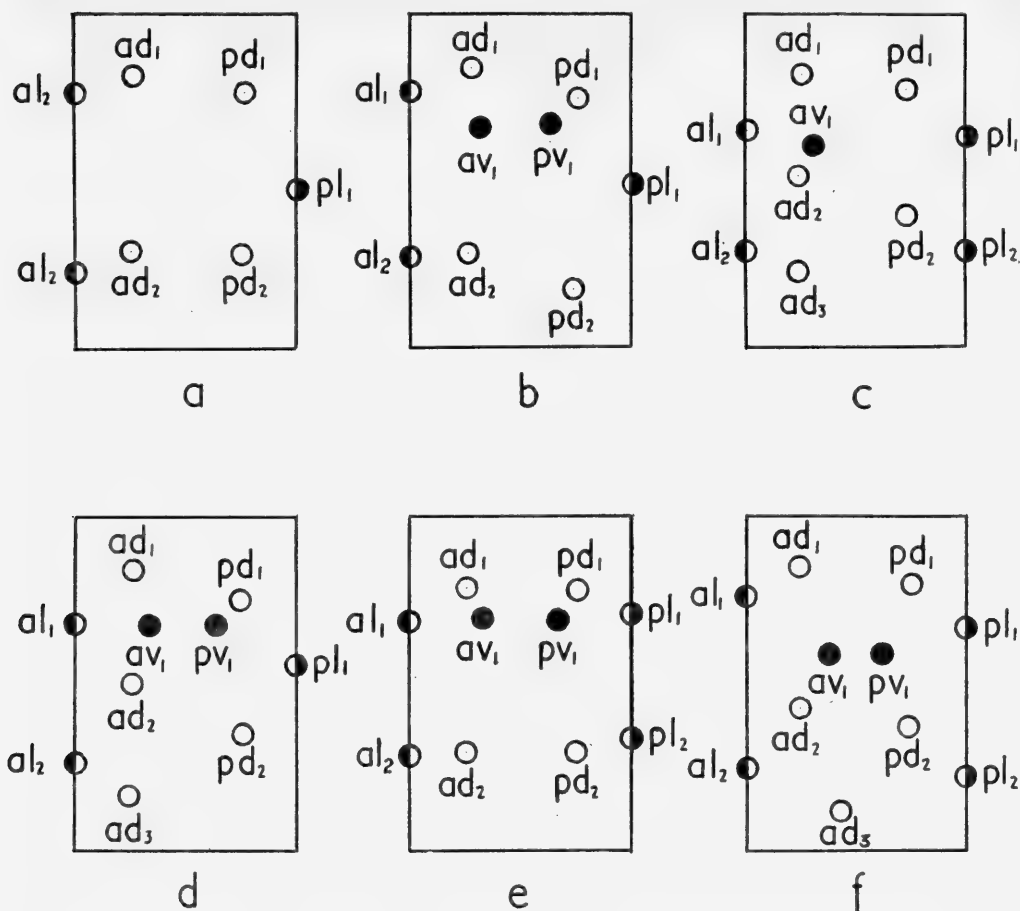
In this type there are no ventral setae (Text-fig. 10a) ; the chaetotaxy comprising setae al_1 , al_2 , ad_1 , ad_2 , pd_1 , pd_2 and pl_1 . It occurs in the majority of the Phytoseiidae.

IX-type ($2 - \frac{2}{1}, \frac{2}{1} - 1$).

I have, to date, only observed this pattern in *Amblyseius graminis* Chant (Phytoseiidae). The chaetotaxy shows an addition of two ventral setae (av_1 and pv_1) to the VII-type (Text-fig. 10b).

Xa-type ($2 - \frac{2}{1}, \frac{2}{1} - 2$).

This differs from the IX-type in having two postero-lateral setae (Text-fig. 10e). This pattern is characteristic of the Microsejidae.



FIGS. 10a-f. Diagrammatic representations of the chaetotaxy of genus II in the free-living Gamasina. a, VII-type (Phytoseiidae). b, IX-type (*Amblyseius graminis* Chant : Phytoseiidae). c, Xc-type (*Sejus* : Aceosejidae). d, Xb-type (Aceosejidae). e, Xa-type (Microsejidae). f, XI-type (Parasitidae).

Abbreviations as in Fig. 1.

Xb-type ($2-\frac{3}{1}, \frac{2}{1}-1$).

This type (Text-fig. 10d) which occurs in the genera *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae) is characterized by having two antero-laterals (al_1 and al_2), five dorsals (ad_{1-3} and pd_{1-2}), two ventrals (av_1 and pv_1) and one postero-lateral (pl_1).

Xc-type ($2-\frac{3}{1}, \frac{2}{0}-2$).

The Xc-type has two postero-laterals but only one ventral seta (Text-fig. 10c). It occurs in the genera *Sejus*, *Platyseius* and *Plesiosejus* (Aceosejidae).

Xd-type ($1-\frac{3}{1}, \frac{2}{1}-2$).

This pattern differs from all others on genus II in having only one antero-lateral seta. I have observed this chaetotaxy in the genus *Thinoseius* (Eviphididae) only.

XI-type ($2-\frac{3}{1}, \frac{2}{1}-2$).

The XI-type (Text-fig. 10f) is by far the most widely distributed chaetotactic pattern of this segment and occurs in the families Parasitidae, Veigaiidae, Arctacaridae, Rhodacaridae, Zerconidae, Epicriidae, Macrochelidae, Pachylaelaptidae, Laelaptidae, Ameroseiidae and Eviphididae (excluding *Thinoseius*) and in the genera *Lasioseius*, *Leioseius*, *Melichares* and *Proctolaelaps* (Aceosejidae).

Tibia II

In the species I have examined, tibia II bears seven, nine or ten setae.

VII-type ($1-\frac{2}{1}, \frac{1}{1}-1$).

This type is characteristic of the Phytoseiidae and comprises setae $al_1, ad_1, ad_2, pd_1, pl_1, av_1$ and pv_1 (Text-fig. 11a).

IXa-type ($1-\frac{2}{1}, \frac{2}{1}-2$).

This type, observed only in *Thinoseius* (Eviphididae), has one antero-lateral seta (al_1).

IXb-type ($2-\frac{2}{1}, \frac{2}{1}-1$).

The chaetotaxy comprises $al_1, al_2, ad_1, ad_2, pd_1, pd_2, pl_1, av_1$ and pv_2 (Text-fig. 11b). This type occurs in the genera *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae).

IXc-type ($2-\frac{2}{1}, \frac{1}{1}-2$).

The chaetotaxy comprises setae $al_1, al_2, ad_1, ad_2, pd_1, pl_1, pl_2, av_1, pv_1$ (Text-fig. 11c). I have observed this type in the genera *Platyseius* and *Plesiosejus* (Aceosejidae).

IXd-type ($2-\frac{1}{1}, \frac{2}{1}-2$).

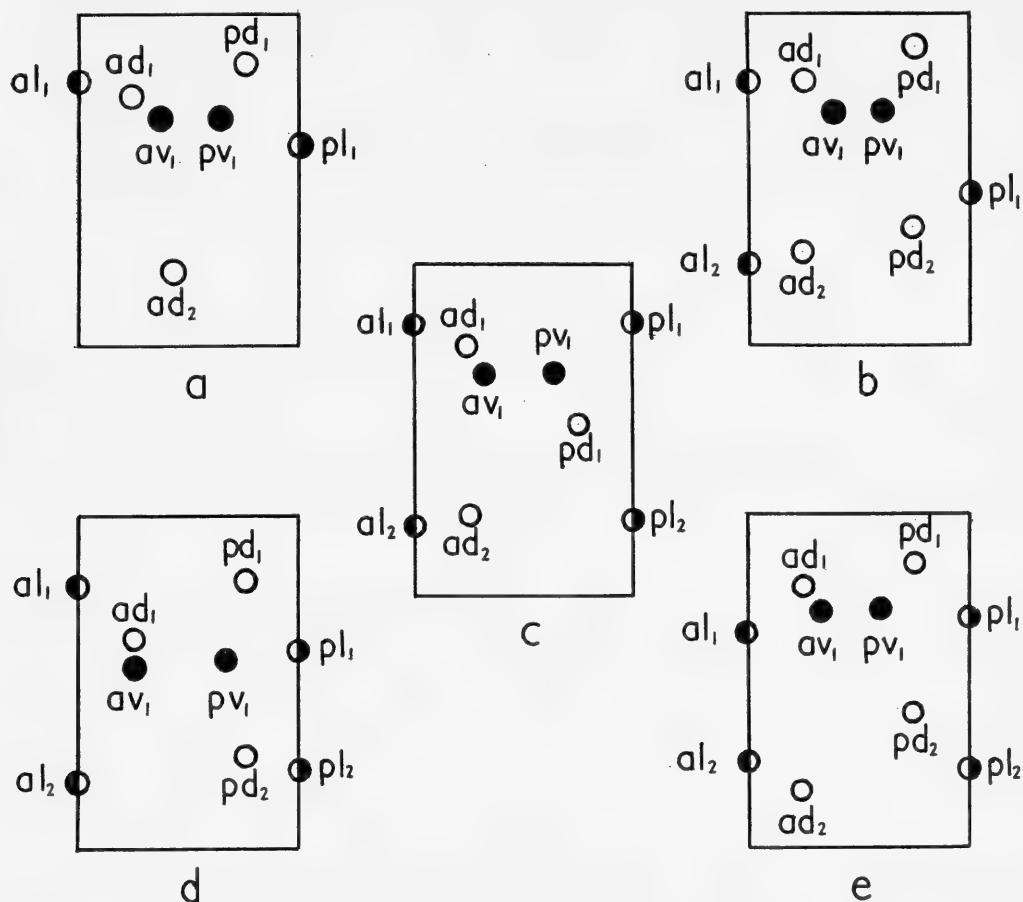
This differs from the IXc-type in the setation of the dorsal surface of the segment; the three setae being ad_1, pd_1 and pd_2 (Text-fig. 11d). It occurs only in the Microsejidae.

X-type ($2-\frac{2}{1}, \frac{2}{1}-2$).

The following setae are present: $al_1, al_2, ad_1, ad_2, pd_1, pd_2, pl_1, pl_2, av_1$ and pv_1 (Text-fig. 11e). This chaetotactic pattern is present in the families Parasitidae, Veigaiidae, Arctacaridae, Rhodacaridae, Zerconidae, Epicriidae, Laelaptidae, Ameroseiidae, Macrochelidae, Pachylaelaptidae, Eviphididae (excluding *Thinoseius*) and in the genera *Lasioseius*, *Leioseius*, *Melichares*, *Proctolaelaps* and *Sejus* (Aceosejidae).

Tarsi II-IV

The chaetotaxy of tarsi II-IV is extremely constant throughout the free-living Gamasina; the details given for *Pergamasus* (p. 278) being applicable throughout. There is some variation in the relative position of the setae due, in some instances, to the elongation of the segment and in the form of setae ad_1 and pd_1 .



FIGS. 11a-e. Diagrammatic representations of the chaetotaxy of tibia II in the free-living Gamasina. a, VII-type (Phytoseiidae). b, IXb-type (*Zerconopsis*: Aceosejidae). c, IXc-type (*Platyseius*: Aceosejidae). d, IXd-type (*Microsejidae*). e, X-type (*Laelaptidae*).

Abbreviations as in Fig. 1.

Femur III

The number of setae on femur III is markedly constant. With the exception of *Thinoseius*, all the species I have examined have six setae (Text-fig. 9e). Owing to the difference in shape of this segment in certain species, the distribution of the setae is subject to some variation. In *Thinoseius*, seven setae are present; the additional seta apparently being developed ventrally (Text-fig. 9f).

Genu III

This segment bears six to ten setae.

VI-type ($1-\frac{2}{0}, \frac{2}{0}-1$).

The following setae are present: al_1 , ad_1 , ad_2 , pd_1 , pd_2 and pl_1 (Text-fig. 12a). There are no ventral setae. I have seen this type only in the genus *Phytoseius* (Phytoseiidae).

VII-type ($1-\frac{2}{1}, \frac{2}{0}-1$).

The chaetotaxy comprises setae al_1 , ad_1 , ad_2 , pd_1 , pd_2 , pl_1 and av_1 (Text-fig. 12b). It occurs in members of the family Macrochelidae and in the genera *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae), *Pachylaelaps* and *Olopachys* (Pachylaelaptidae), *Thinoseius* (Eviphididae) and *Iphiseius* and *Typhlodromus* (Phytoseiidae).

VIIIa-type ($1-\frac{2}{1}, \frac{2}{1}-1$).

The chaetotaxy differs from the VII-type in the addition of pv_1 (Text-fig. 12c). This chaetotactic pattern occurs in the Eviphididae (excluding *Thinoseius*).

VIIIb-type ($2-\frac{2}{1}, \frac{2}{0}-1$).

This chaetotactic pattern has been found in the genera *Asca* and *Saprolaelaps* (Rhodacaridae), *Sejus*, *Platyseius* and *Plesiosejus* (Aceosejidae), *Pachyseius* (Pachylaelaptidae) and *Epicriopsis* (Ameroseiidae). The eight setae comprise al_1 , al_2 , ad_1 , ad_2 , pd_1 , pd_2 , pl_1 and av_1 (Text-fig. 12d).

IXa-type ($2-\frac{2}{1}, \frac{2}{1}-1$).

Setae al_1 , al_2 , ad_1 , ad_2 , pd_1 , pd_2 , pl_1 , av_1 and pv_1 are present in this type (Text-fig. 12e). This pattern occurs in the families Parasitidae, Veigaiaidae, and in the genera *Rhodacarus*, *Rhodacarellus*, *Cyrtolaelaps*, *Euryparasitus*, *Gamasellus*, *Hydrogamasus*, *Ologamasus* and *Gamasiphis* (Rhodacaridae), *Lasioseius*, *Leioseius*, *Melichares* and *Proctolaelaps* (Aceosejidae), *Hypoaspis*, *Coleolaelaps* and *Ololaelaps* (Laelaptidae) and *Neocypholaelaps* (Ameroseiidae).

IXb-type ($2-\frac{2}{1}, \frac{2}{0}-2$).

I have observed this type only in the Microsejidae (Text-fig. 12f).

X-type ($2-\frac{2}{1}, \frac{2}{1}-2$).

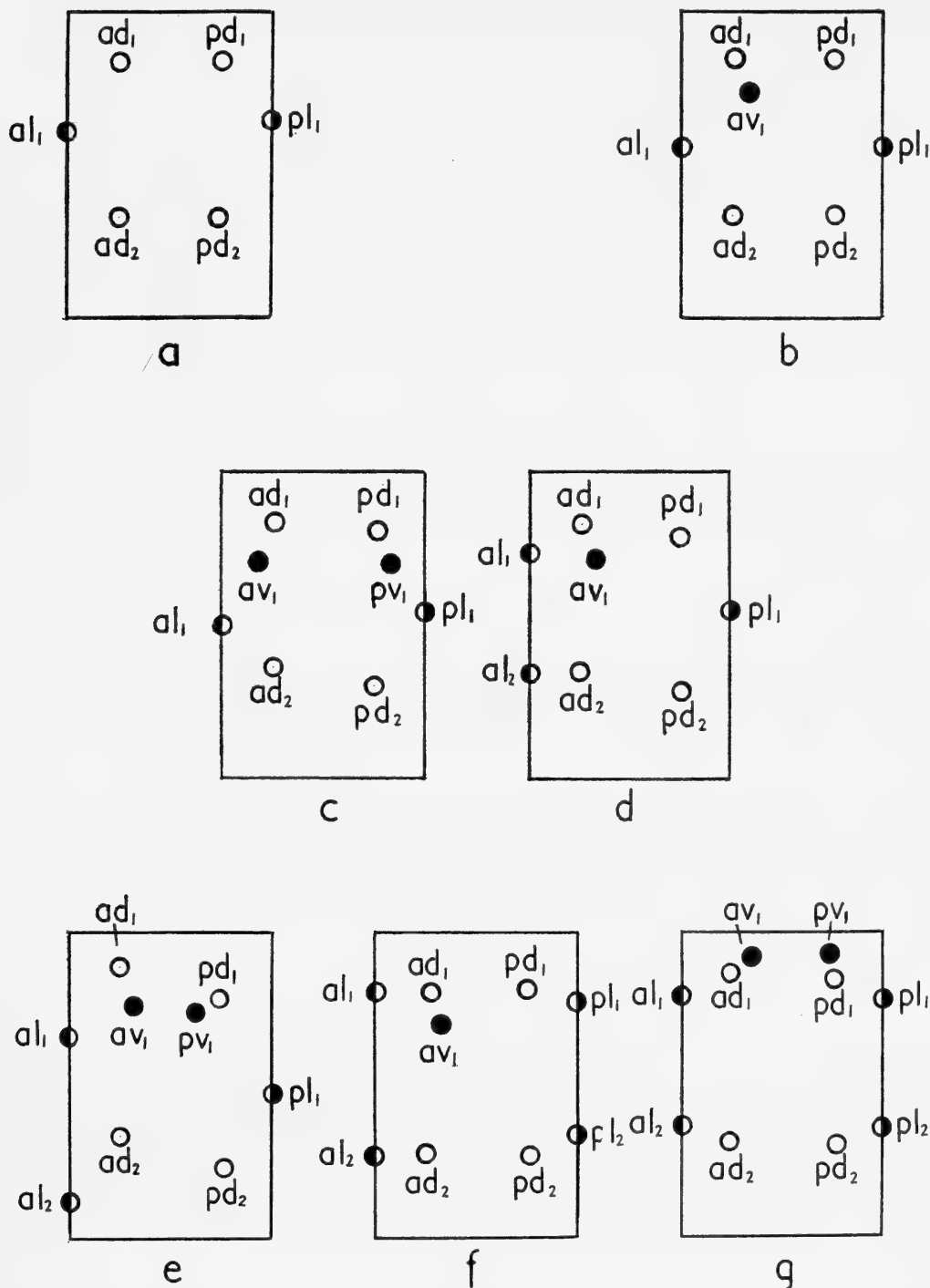
The ten setae comprise al_1 , al_2 , ad_1 , ad_2 , pd_1 , pd_2 , pl_1 , pl_2 , av_1 and pv_1 (Text-fig. 12g). It occurs in the families Arctacaridae, Zerconidae and Epicriidae, and in the genera *Ameroseius* and *Kleemannia* (Ameroseiidae).

Tibia III

The following three types of chaetotactic pattern have been observed on this segment:

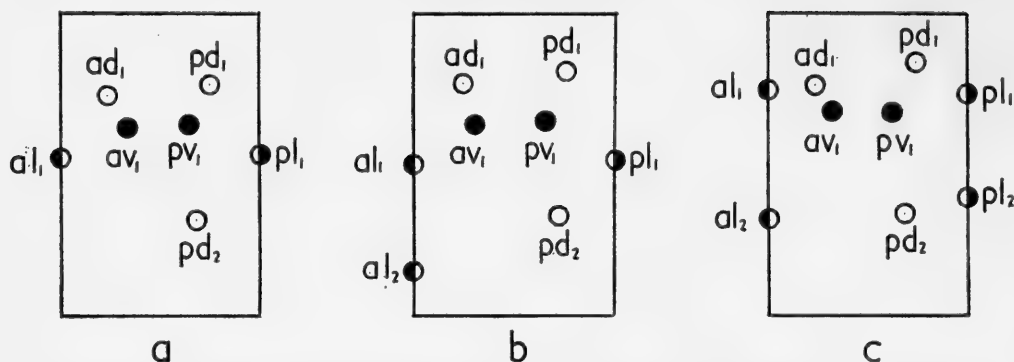
VII-type ($1-\frac{1}{1}, \frac{2}{1}-1$).

This type occurs in the families Phytoseiidae, Eviphididae, Macrochelidae and Pachylaelaptidae, and in the genera *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae). The chaetotaxy comprises al_1 , ad_1 , pd_1 , pd_2 , pl_1 , av_1 and pv_1 (Text-fig. 13a).



FIGS. 12a-g. Diagrammatic representations of the chaetotaxy of genu III in the free-living Gamasina. a, VI-type (*Phytoseius*: Phytoseiidae). b, VII-type (Macrochelidae). c, VIIIa-type (Eviphididae). d, VIIIb-type (*Asca*: Rhodacaridae). e, IXa-type (Parasitidae). f, IXb-type (Microsejidae). g, X-type (Zerconidae).

Abbreviations as in Fig. 1.



FIGS. 13a-c. Diagrammatic representations of the chaetotaxy of tibia III in the free-living Gamasina. **a**, VII-type (Phytoseiidae). **b**, VIII-type (Parasitidae). **c**, IX-type (Microsejidae).

Abbreviations as in Fig. 1.

VIII-type ($2-\frac{1}{1}, \frac{2}{1}-1$).

There is an addition of one antero-lateral seta to the VII-type; the seta being al_2 (Text-fig. 13b). This pattern is present in the families Parasitidae, Veigaiaidae, Rhodacaridae, Laelaptidae, Ameroseiidae (excluding *Kleemannia*) and in the genera *Lasioseius*, *Leioseius*, *Melichares* and *Proctolaelaps* (Aceroseiidae).

IX-type ($2-\frac{1}{1}, \frac{2}{1}-2$).

Seta pl_2 is additional to the VIII-type (see Text-fig. 13c). It occurs in the families Arctacaridae, Zerconidae, Epicriidae and Microsejidae and in the genus *Kleemannia* (*Ameroseiidae*).

Femur IV

The presence of six setae on this segment is extremely constant in the free-living Gamasina; the only exception being members of the Microsejidae. In the majority of the species I have examined the chaetotaxy comprises al_1 , ad_1 , ad_2 , pd_1 , pl and v_1 (Text-fig. 9h) but there are variants of this pattern as, for example, in the aceroseiid *Plesioseius* (Text-fig. 9g) which has four dorsals but no postero-lateral setae. The microsejids have seven setae on this segment (al_1 , ad_1 , ad_2 , pd_1 , pd_2 , av_1 and pv_1).

Genu IV

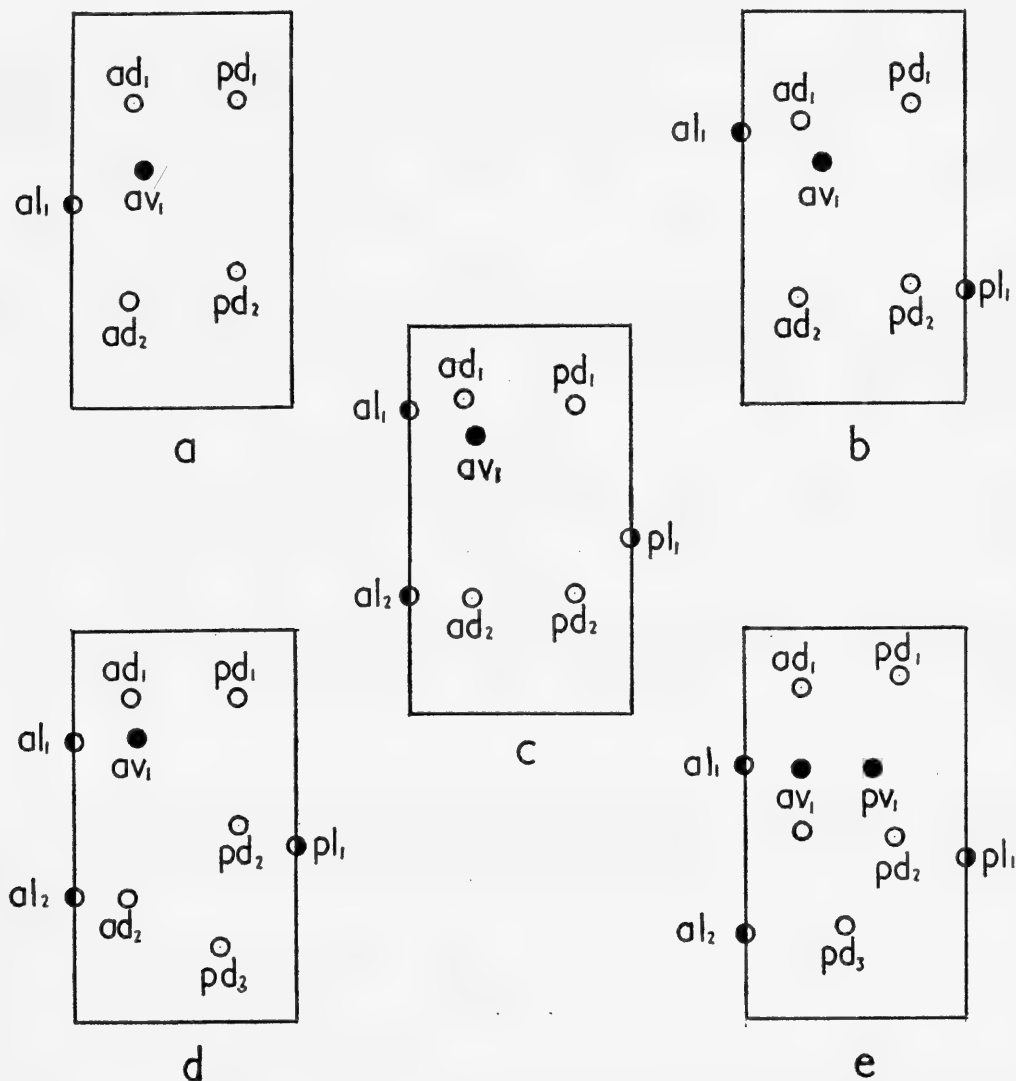
Five types of chaetotaxy of genu IV have been observed.

VI-type ($1-\frac{2}{1}, \frac{2}{0}-0$).

The following setae are present: al_1 , ad_1 , ad_2 , pd_1 , pd_2 and av_1 (Text-fig. 14a). This pattern is found in certain species of the genus *Macrocheles* s.lat. (Macrochelidae) and has been used as a taxonomic character by Evans & Hyatt (1962).

VII-type ($1-\frac{2}{1}, \frac{2}{0}-1$).

This shows an addition of seta *pl* to the VI-type (Text-fig. 14*b*). It is found in the families Pachylaelaptidae, Eviphididae and Phytoseiidae, in the genera *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae), *Digamasellus* (Rhodacaridae) and certain species of the Macrochelidae.



FIGS. 14*a-e*. Diagrammatic representations of the chaetotaxy of genus IV in the free-living Gamasina. *a*, VI-type (*Macrocheles*: Macrochelidae). *b*, VII-type (Eviphididae). *c*, VIII-type (Microsejidae). *d*, IX-type (*Lasioseius*: Aceosejidae). *e*, X-type (Parasitidae).

Abbreviations as in Fig. 1.

VIII-type ($2-\frac{2}{1}, \frac{2}{0}-1$).

Setae al_1 , al_2 , ad_1 , ad_2 , pd_1 , pd_2 , pl_1 and av_1 are present (Text-fig. 14c). This type occurs in the family Microsejidae.

IX-type ($2-\frac{2}{1}, \frac{3}{0}-1$).

Seta pd_3 is added to the VIII-type (Text-fig. 14d). It is found in the families Laelaptidae, Ameroseiidae and in the genera *Lasioseius*, *Leioseius*, *Melichares*, *Proctolaelaps*, *Sejus*, *Platyseius* and *Plesiosejus* (Aceosejidae), and in *Asca* and *Halolaelaps* (Rhodacaridae).

X-type ($2-\frac{2}{1}, \frac{3}{1}-1$).

This type (Text-fig. 14e) has two ventral setae (pv_1 being additional to the ventral chaetotaxy found in the other types). It occurs in the families Parasitidae, Veigaiaidae, Arctacaridae, Zerconidae, Epicriidae and in the genera *Rhodacarus*, *Rhodacarellus*, *Cyrtolaelaps*, *Euryparasitus*, *Gamasellus*, *Ologamasus*, *Hydrogamasus* and *Gamasiphis* (Rhodacaridae).

Tibia IV

Six types of chaetotaxy of tibia IV have been observed; the number of setae on the segment ranging from six to ten.

VI-type ($1-\frac{1}{1}, \frac{2}{0}-1$).

This type comprising setae al_1 , ad_1 , pd_1 , pd_2 , pl_1 and av_1 occurs in members of the family Phytoseiidae (Text-fig. 15a).

VII-type ($1-\frac{1}{1}, \frac{2}{1}-1$).

The chaetotaxy of this type differs from VI in the addition of one postero-ventral seta (Text-fig. 15b). It is found in the families Macrochelidae, Pachylaelaptidae and Eviphididae, and in the genera *Arctoseius*, *Iphidozercon* and *Zerconopsis* (Aceosejidae) and *Digamasellus* (Rhodacaridae).

VIII-type ($2-\frac{1}{1}, \frac{2}{1}-1$).

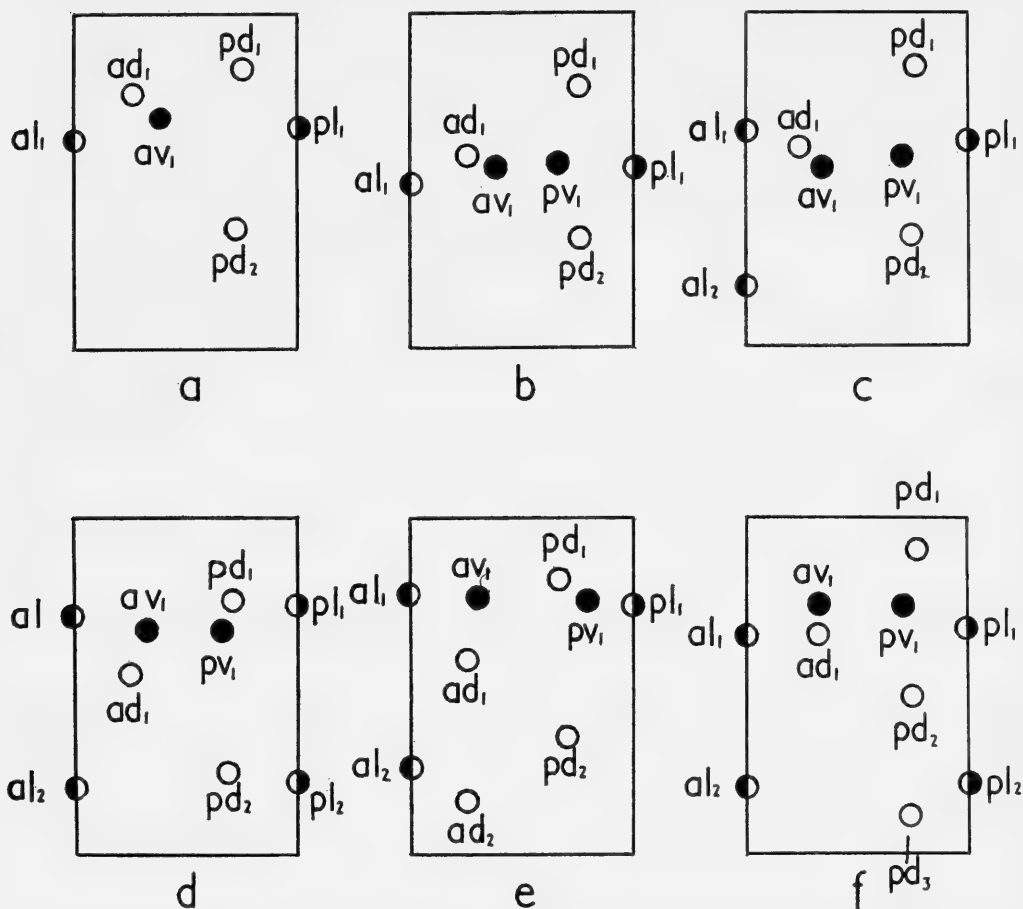
I have found this type in the genus *Halolaelaps* (Rhodacaridae) and the chaetotactic pattern differs from the VII-type in the addition of seta al_2 (Text-fig. 15c).

IXa-type ($2-\frac{2}{1}, \frac{2}{1}-1$).

The chaetotaxy comprises al_1 , al_2 , ad_1 , ad_2 , pd_1 , pd_2 , pl_1 , av_1 and pv_1 (Text-fig. 15e). The pattern occurs in the family Ameroseiidae.

IXb-type ($2-\frac{1}{1}, \frac{2}{1}-2$).

In contrast to type IXa, the segment bears only one antero-dorsal seta (ad_1) but two postero-lateral setae (pl_1 and pl_2). This type of chaetotaxy occurs in the families Zerconidae and Microsejidae (Text-fig. 15d).



FIGS. 15a-f. Diagrammatic representations of the chaetotaxy of tibia IV in the free-living Gamasina. *a*, VI-type (Phytoseiidae). *b*, VII-type (Eviphididae). *c*, VIII-type (Halolaelaps: Rhodacaridae). *d*, IXb-type (Microsejidae). *e*, IXa-type (Ameroseiidae). *f*, X-type (Parasitidae).

Abbreviations as in Fig. 1.

X-type ($2-\frac{1}{1}, \frac{3}{1}-2$).

This type shows an addition of postero-dorsal seta (pd_3) to the setal complement of IXb (Text-fig. 15f). It is found in the families Parasitidae, Veigaiaidae, Arctacaridae, Epicriidae and Laelaptidae and Aceosejidae (excluding genera under VII-type), and in the genera *Rhodacarus*, *Rhodacarellus*, *Cyrtolaelaps*, *Euryparasitus*, *Gamasellus*, *Ologamasus*, *Hydrogamasus* and *Gamasiphis*.

DISCUSSION

The wide variety of leg segmental chaetotactic patterns displayed by the free-living Gamasina will undoubtedly provide useful morphological criteria for their classification. Taxonomic characters based on chaetotactic patterns are readily definable quan-

titatively and are thus suitable for mathematical analysis. The value of chaetotactic patterns as indicators of phylogenetic relationships is difficult to assess although in free-living forms their stability at species, genus and family levels is surprisingly high. However, the nature of the ontogenetic development of the chaetotaxy, particularly the importance of localized neoteny in determining specific segmental patterns in specialized parasitic forms, allows for the widespread occurrence of convergence in chaetotactic patterns. The results of the present study suggest that the overall chaetotaxy of the legs, especially of legs I and II, may be of significance in the classification of the suborder at familial and suprafamilial levels whereas differences in the chaetotaxy of individual segments may be of more value at species and genus level.

Segmental chaetotaxy of the legs appears to be subject to little or no intraspecific variation. In the free-living Gamasina, differences in chaetotactic patterns between species of the same genus are usually restricted to a single segment as, for example, the presence of six or seven setae on genu IV in *Macrocheles* (Evans & Hyatt, 1962). Specialized parasitic forms exhibit considerably more interspecific variation. According to Till (1962), species of the genus *Androlaelaps* show differences in the chaetotaxy of tibia I, tibia III, genu III and genu IV. This variability is even more marked in the endoparasitic forms where differences in overall leg chaetotaxy may be of importance only at species level. Differences in the chaetotaxy of one or two leg segments are also evident at generic level and are particularly useful in providing "key characters" for the differentiation of genera belonging to the same family. For example, the chaetotactic patterns of genu III in the Ameroseiidae, of genua III and IV in the Phytoseiidae and genu III in the Pachylaelaptidae.

An analysis of the leg chaetotaxy in confamilial genera indicates a greater stability in the chaetotaxy of legs I and II than of legs III and IV. With few exceptions, the familial concepts based on leg chaetotaxy support the present classification of the free-living Gamasina based on other morphological criteria. The notable exception is the family Rhodacaridae. The genera *Rhodacarus*, *Rhodacarellus*, *Cyrtolaelaps*, *Euryparasitus*, *Gamasellus*, *Ologamasus*, *Gamasiphis*, *Hydrogamasus* and *Sessiluncus* form a natural assemblage which can be accommodated in the family Rhodacaridae, whereas the genera *Digamasellus*, *Asca* and *Halolaelaps* do not appear to be confamilial with the *Rhodacarus*-group. Their affinities appear to be with certain genera of the Aceosejidae but whether they should be placed in that family or in a distinct family (Digamasellidae) can only be decided by a comprehensive study of the complex. Certainly the emphasis placed on the nature of the dorsal sclerotization of the idiosoma in the classification is not justified in the light of the conclusions reached on the basis of chaetotactic studies.

The criterion of leg chaetotaxy also gives interesting results when applied to the classification of the Aceosejidae. At present this family is divided into two sub-families (Evans, 1957), namely, the Aceosejinae and Platyseiinae. On the bases of segmental patterns, however, three groups of genera may be recognized of which two groups are more closely related to each other than to the third. The three groups are: (a) *Lasioseius*, *Leioseius*, *Proctolaelaps*, *Melichares* and *Zercoseius* (Aceosejinae); (b) *Sejus*, *Platyseius* and *Plesiosejus* (Platyseiinae) and (c) *Arctoseius*, *Iphidozercon*

and *Zerconopsis*. In group (c) the genera *Arctoseius* and *Iphidozercon* are at present placed in the Aceosejinae and *Zerconopsis* in the Platysejinae. This revised grouping of the genera appears to be more satisfactory since members of group (c) which may be referred to as the Arctoseiinae, differ from the other two groups in the nature of the chaetotaxy of the opisthonotal region of the dorsal shield in the female. The Arctoseiinae also show affinities with the *Digamasellus*-group mentioned above.

The chaetotaxy of legs I and II also provide good "key characters" for the separation of certain families which have been difficult to distinguish on such characters as idiosomal sclerotization and chaetotaxy. Two such cases immediately come to mind, namely, the separation of the Aceosejidae and Phytoseiidae, and of the Eviplididae and Laelaptidae. Reference to the chaetotactic patterns of the genua and the tibiae of legs I will now remove much of the uncertainty associated with the recognition of members of these families in existing key works.

The results of isolated observations on the leg chaetotaxy of the Uropodina and Antennophorina (or Fedrizzina) suggest that segmental chaetotaxy is also of importance at all levels of their classification. In the Uropodina, for example, there is a marked and constant difference between the segmental chaetotaxy of the Lower Uropodina (Trachytid-type) and the more specialized Higher Uropodina (Uropodid-type); the latter exhibiting considerably more localized neoteny in leg chaetotaxy to the extent of certain segments retaining the larval chaetotaxy in the adult stages. A comprehensive study of the leg chaetotaxy in the Uropodina is now being undertaken by Mr. Brian Ainscough.

The Mesostigmata, in common with the Anactinochaeta as a whole, display little variety in setal types. Unlike the Actinochaeta which have a variety of setal types that can be distinguished on the basis of their optical and chemical properties (Grandjean, 1935), the setae of the leg segments of the Mesostigmata referred to in the present work appear to be of one type. They are solid and lack "actinochitin". The sensory field distally on tarsus I, however, has a variable number of hollow setae which bear a superficial resemblance to the solenidia of certain Actinochaeta.

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A REVISION OF THE RECENT ROUND HERRINGS

(PISCES: DUSSUMIERIIDAE)



P. J. P. WHITEHEAD

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ZOOLOGY

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P. J. P. WHITEHEAD

Department of Zoology, British Museum (Natural History)



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SYNOPSIS

The recent round herrings, the Dussumieriidae, are here maintained as a family distinct from the Clupeidae or true herrings. Two subfamilies are recognized, the Dussumieriinae containing the genera *Dussumieria* and *Etrumeus*; and the Spratelloidinae, which is further split into the tribes Spratelloidini and Ehiravini. The former contains the genera *Spratelloides* and *Jenkinsia*, and the latter *Ehirava*, *Gilchristella* and *Sauvagella*.

In those genera with a wide distribution (e.g. *Dussumieria*, *Etrumeus*, *Spratelloides*), morphometric and meristic data, from samples covering the entire geographical range, indicate that many former species are no more than geographical variants, or in some cases subspecies. Ten species are recognized, and these are described and figured. Keys are given for all taxa.

The systematics and phylogeny of the Dussumieriidae are examined in the light of certain hitherto neglected characters, principally the development of abdominal and pelvic scutes, the formation of the posterior cranial fontanelles, the shape of the cleithral outline of the gill opening, the shape of the bones in the opercular series, and the number and shape of the supra-maxillary bones. It is concluded that the Dussumieriidae are modern representatives of a primitive non-scuted clupeid.

INTRODUCTION

THE Dussumieriidae, or round herrings, are small clupeid fishes fairly widely distributed in tropical and temperate seas, mainly in the Indo-Pacific region. They are usually separated from the Clupeidae by their absence of abdominal scutes, thus having rounded rather than keeled bellies. Jordan & Gilbert (1883), Günther (1868), and Weber & de Beaufort (1913), among earlier writers, placed the round herrings as a subfamily of the Clupeidae, but nowadays they are usually given family status (e.g. since Jordan, 1925). Svetovidov (1952) however retained them in a subfamily of the Clupeidae, but the absence of scutes in all but one species of round herring is here considered evidence that the evolution of this group predated the evolution of the scuted clupeid groups.

The most recent revision of the family was that of Bertin (1943), who recognized eight genera containing recent species within two subfamilies, the Dussumieriinae and the Spratelloidinae. I have here rejected three of these genera (*Montalbania*, *Perkinsia* and *Halecula*) but have accepted two others (*Ehirava* and *Jenkinsia*). Comparatively little systematic work has been published recently on the group, being for the most part descriptions of species and some notes on bionomics. Chapman (1948) published a useful description of the osteology of the round herrings, comparing them with the clupeids, but considered only a single genus, *Etrumeus*. Ridewood (1904) had earlier compared the skull of *Dussumieria* with certain clupeoids, but scarcely any work has been done on the osteology of the spratelloidine round herrings (except caudal anatomy by Hollister, 1936).

The recent discovery of abdominal scutes in a round herring (Whitehead, 1962a) raises the problem of the relationship of the Dussumieriidae to the Clupeidae; it has also thrown more light on the division between the Spratelloidinae and the Dussumieriinae. I have found here that, although the Spratelloidinae approach the Clupeidae in many respects, and especially in the form of the pelvic scute, those species which most closely approach the Clupeidae are at the same time those which also most closely resemble the Dussumieriinae in other characters. On the other hand, in certain characters the division between the Spratelloidinae and the Dussumieriinae is as marked as is the division between either and the Clupeidae. But

the presence or absence of scutes seems to me to be of such fundamental importance that the round herrings should be separated from the clupeids at family level.

Although Gosline (1951) drew attention to the Ruling of the International Commission for Zoological Nomenclature concerning the use of the generic name *Stolephorus*, it is worth repeating that, under Opinion 93, the genotype of *Stolephorus* Lacépède is *S. commersonianus*¹ Lacépède, by description and figure an undeniable anchovy, so that *Spratelloides* Bleeker must replace *Stolephorus* as a round herring genus, and the round herrings are the Dussumieriidae, not the Stolephoridae, as Fowler (1941, 1958), Smith (1955), and others have termed them. The error arose through an inadequate description by Houttuyn of a fish later included by Lacépède in his engraulid genus *Stolephorus*; this is discussed further on p. 340.

This revision is based on collections in the British Museum (Natural History) and on material lent or donated by other institutions, for which I would like to thank particularly, Dr. R. Rosenblatt of the Scripps Institute of Oceanography; Professor C. R. Robbins of the Institute of Marine Studies, University of Miami; Professor J. L. B. Smith of Rhodes University; Mr. A. Ben-Tuvia, of the Sea Fisheries Research Station, Haifa; Dr. L. Woods of the Chicago Natural History Museum; Dr. M. Blanc of the Museum Nationale d'Histoire Naturelle, Paris; Dr. J. Nielsen, Universitetets Museum, Copenhagen, and Dr. H. Steinitz of the Hebrew University, Jerusalem.

Family DUSSUMIERIIDAE

Diagnosis

Clupeoid fishes usually with elongate, fusiform bodies and rounded bellies (body more compressed in the tribe Ehiravini). One or two abdominal scutes associated with the pelvic fin; pre- or post-pelvic scutes entirely absent except for the former in one instance (*Gilchristella aestuarius*); neither the pelvic scutes nor, where present, the pre-pelvic scutes are keeled.

Anal fin normally equal to or shorter than dorsal, exceptionally longer. Pelvics slightly in front, below or a little behind dorsal. Pectorals set low on body. Anal always behind dorsal.

Mouth terminal, lower jaw more or less projecting. Premaxilla small, edentulous or with a single series of small conical teeth which are often deciduous. Small, conical and sometimes deciduous teeth on dentary, along lower edge of maxilla, on glossohyal, suprabasal (where present), mesopterygoids and palatine. A well-developed posterior supra-maxilla overlapping distal tip of maxilla and produced anteriorly into a pointed shaft; a second, plate-like supra-maxilla sometimes present, lying between the shaft and the upper edge of the maxilla.

Hyomandibular with two separate cranial heads articulating with both sphenotic and pterotic; ceratohyal with or without indented ventral edge. Branchiostegal rays from six to twenty.

Pseudobranchiae well-developed; gill membranes separate, free from isthmus; gillrakers fine and slender but rarely more than about forty. Pyloric caecae numerous. Adipose tissue often entirely covering eye.

¹ A cheironym which should be rejected in favour of the name actually used by Lacépède, *commersonii*.

Sensory canals of head well-developed, with superficial ramifications extending on to pre-operculum, sub-orbitals, operculum, and sometimes on to maxilla, part of articular, and sub-operculum.

Scales cycloid, covering entire body except head, often highly deciduous; elongate axillary scales in angle of pectoral and pelvic fins and elongate scales on upper and lower lobes of caudal. Vertebrae 30-56.

The Dussumieriidae are small, often brilliantly silvery fishes chiefly found in the Indo-Pacific region between latitudes 40° N. and 40° S., but with a few species along the Pacific and Atlantic coasts of North America. They are found in coastal regions and in estuarine and tidal lagoons and, although rarely exploited by any large fishery, they are acceptable in some places as food fishes when caught in sufficient number. One of the three fishes constituting the "Iwashi" fishery of Japan, is the round herring, *Etrumeus*.

The Dussumieriidae fall into two very distinct groups, the Dussumieriinae, larger fishes with more branchiostegal rays (14-19); and the Spratelloidinae, comprising species which rarely exceed 110 mm. and have 6-7 branchiostegal rays. The former subfamily appears to be the more primitive, while the latter approaches the Clupeidae so nearly in certain cases (e.g. *Gilchristella aestuarius*), that it would be tempting to place the Spratelloidinae with the clupeids were it not for the closely related but more typical spratelloidines, such as *Spratelloides gracilis*.

- I. Branchiostegal rays 14-19; adult size 150-350 mm.; pelvic scute w-shaped; no posterior cranial fontanelles in adults; ceratohyal not excavated ventrally; dorsal rays 16-21 **Dussumieriinae**
- II. Branchiostegal rays 6-7; adult size 50-110 mm.; pelvic scute often with ascending process; a pair of posterior cranial fontanelles in adults of most species; ceratohyal excavated ventrally; dorsal rays 11-16 **Spratelloidinae**

Subfamily DUSSUMIERIINAE

Diagnosis

Dussumieriid fishes, with 14-19 branchiostegal rays, the first seven to nine attached to the ceratohyal whose ventral edge is not excavated. Premaxilla toothed, teeth not deciduous; maxilla with a narrow posterior supra-maxilla whose depth is about half that of the maxilla at its widest point; a second, anterior supra-maxilla present in some cases. Ventral scutes absent except for a modified w-shaped scute surrounding the base of the pelvic fins and sometimes a second triangular, plate-like scute immediately behind the pelvics.

No posterior cranial fontanelles in adults, this portion of the head forming a shallow, triangular depression. Posterior margin of pre-operculum not vertical but inclined forwards; ventral margin of operculum not horizontal but rising posteriorly.

A small, usually little developed, fleshy eminence on the postero-ventral angle of the cleithrum. Inter-operculum barely exposed in lateral view.

Dorsal rays 16-21; anal 9-19. Transverse scales on body 11-15. Vertebrae 52-56.

Adult size 150–350 mm.

Two genera, *Dussumieria* and *Etrumeus*.

- A. Pelvic fins under dorsal base; two supra-maxillae present; anal rays 14–19;
exposed portion of sub-operculum sub-rectangular *Dussumieria*
- B. Pelvic fins behind dorsal base; a single supra-maxilla; anal 9–13; exposed portion
of sub-operculum triangular *Etrumeus*

Etrumeus and *Dussumieria* are obviously closely related, but Fowler (1958) used the differences in pelvic position, number of anal rays, and presence or absence of a second supra-maxilla to erect a tribal division in the Dussumieriinae. This does not seem justified and the differences between these two genera are small compared with those used here to split the Spratelloidinae into two tribes (p. 329).

Genus *DUSSUMIERIA* Valenciennes

Dussumieria Valenciennes, 1847, *Hist. Nat. Poiss.*, 20: 467 (Type: *Dussumieria acuta* Valenc.).
Montalbiana Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853: 7. (Type: *Etrumeus* (*Montalbiana*) *albulina* Fowler, 1934.)

Body elongate, more or less compressed. Snout pointed, jaws equal. Two supra-maxillae, each about half the length of the maxilla (Text-fig. 28). Proximal half of maxilla thickened along its dorsal edge, distal half flat, tip of maxilla rounded, almost entire ventral edge bearing small conical teeth. Premaxillae toothed. A single w-shaped scute surrounding base of pelvic fins. Dorsal rays 17–21, anal rays 14–19, 20–34 gillrakers on lower part of first gill arch. Branchiostegals 14–20. Vertebrae 54–56. Anal well behind the dorsal, whose origin is a little nearer the caudal base than the tip of the snout. Pelvic origin below middle of dorsal fin. A slight fleshy eminence on the angle of the posterior margin of the cleithrum (cleithral flap), not so developed as in *Spratelloides*, but more developed than that of *Etrumeus* (see Text-fig. 30b). Gill filaments of first arch shortened to accommodate this eminence. Ventral margin of operculum nearer to horizontal than in *Etrumeus* (Text-fig. 30b).

A single species recognized here, *D. acuta*.

This genus is entirely Indo-Pacific in its natural distribution, but since the opening of the Suez Canal there have been several records of *Dussumieria*, and especially the Erythrean form, being caught in the eastern Mediterranean (Lissner, 1949, and Ben-Tuvia, 1953). I have examined twenty such specimens and they have the high gillraker count typical of the Red Sea population (Text-fig. 3). The Red Sea form evidently is not so closely adapted to hot, hypersaline conditions that it cannot survive elsewhere. On the other hand it has been able to survive passage through the even more saline Bitter Lakes. It will be interesting to see whether the Mediterranean population will now lose the rather distinctive characters of the Red Sea form.

Dussumieria acuta Valenciennes

(Text-fig. 5)

- Dussumieria acuta* Valenciennes, 1847, *Hist. Poiss. Nat.*, **20** : 467, pl. 606 (Type locality : Bombay, Coromandel); Cantor, 1849, *J. Asiat. Soc. Beng.*, **18** : 1268; Day, 1865, *Fishes of Malabar* : 226; Kner, 1865, *Reise Novarra, Fische* : 330; Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 466; Bleeker, 1872, *Atlas Ichth. Ind. Néerland.*, **6** : 94, pl. 271, fig. 1; Day, 1878, *Fishes of India*, pt. 4 : 647, pl. 166, fig. 4; Weber and Beaufort, 1913, *Fishes Indo-Aust. Arch.*, **2** : 21, fig. 13; Fowler, 1928, *Mem. Bernice P. Bishop Mus.*, **10** : 30; Roxas, 1934, *Philipp. J. Sci.*, **55** : 251, pl. 1, fig. 5; Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 570; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 3, figs. 1 (scale) and 2; Liang, 1948, *Quart. J. Taiwan Mus.*, **1** : 2; Monroe, 1955, *Marine and freshwater fish. Ceylon* : 28; Fowler and Steinitz, 1956, *Bull. Res. Council. Israel*, **5 B** (3-4) : 261.
- Dussumieria elopsoidea* Bleeker, 1849, *Verh. Bat. Gen.*, **22** : 12; Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 466.
- Dussumieria hasselti* Bleeker, 1850, *Natuurk. Tijdschr. Ned. Ind.*, **1** : 422; *Idem*, 1872, *Atlas Ichth. Ind. Néerland.*, **6** : 95, pl. 271, fig. 2; Day, 1878, *Fishes of India*, pt. 4 : 647, pl. 166, fig. 5; Weber and Beaufort, 1913, *Fish. Indo-Aust. Arch.*, **2** : 23; Roxas, 1934, *Philipp. J. Sci.*, **55** : 250; Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 572; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 6, fig. 2; Schultz and Wellander, 1953, *Bull. U.S. nat. Mus.*, No. 202 : 25; Monroe, 1955, *Marine and freshwater fish, Ceylon* : 28; Fourmanoir, 1961, *Mem. Inst. sci. Madagascar*, (F) **4** : 84, fig. 1.
- Dussumieria productissima* Chabanaud, 1933, *Bull. Inst. océanogr. Monaco*, No. 627 : 4, figs. 3-6; *Idem*, 1933, *Bull. Soc. zool. France*, **58** : 289; Gruvel and Chabanaud, 1937, *Mém. Inst. égypt. (Égypte)*, **35** : 3, fig. 3; Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 570; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 6; Ben-Tuvia, 1953, *Bull. Sea Fish. Res. Stat., (Israel)*, No. 8 : 6, fig. 1.
- Etrumeus (Montalbana) albulina* Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, **85** : 244, fig. 7; *Idem*, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 574, fig. 14.
- Montalbana albulina* Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 8.

Notes on Synonymy

The most important references are cited here; full synonymies are given by Fowler (1941) under *D. acuta*, *D. productissima*, and *D. hasselti*.

Fowler (1941), Bertin (1943) and Herre (1953) amongst others, have all included *Dussumieria elopsoidea* Bleeker in the synonymy of *D. acuta* Valenciennes, recognizing two further species, *D. hasselti* Bleeker, which extends to the eastern limits of the range of this genus (China), and *D. productissima* Chabanaud from the extreme western fringe (Gulf and Isthmus of Suez). Günther (1868) had, however, placed *D. hasselti* in synonymy with *D. elopsoidea*. Examination of the holotypes of the last two species has revealed no possible basis for specific distinction on preserved characters (see Table I). At the same time, the specimens in this museum labelled *D. acuta* and *D. elopsoidea* (*sensu* Günther) both show a parallel variation in several characters which can clearly be correlated with geographical distribution. Specimens from the intermediate part of the range of these two species could be assigned to either species, and in fact Bertin (1943) stated that all but two of Valenciennes types of *D. acuta* should be referred to *D. hasselti*.¹

¹ I have examined these specimens through the courtesy of Dr. M. Blanc of the Museum Nationale d'Histoire Naturelle, Paris, and wish to thank him for allowing me to borrow them.

Unfortunately Valenciennes did not state the number of scales in lateral series in his *D. acuta*, and neither did Chabanaud for *D. productissima*. The scales in *Dussumieria* are highly deciduous; amongst 29 specimens of *D. acuta* in this museum, there is only one in which a scale count can even be estimated. In this case 36 scales are actually present, but at least 12 scales, more likely 15, are missing but fairly well represented by scale pockets. This would place the fish in the range of *D. elopsooides* (i.e. 52–56 scales; cf. 42–44 reported for *D. acuta*). In the majority of descriptions it is rarely stated whether the scale count is an actual one based on the specimens examined, or whether it merely follows previous descriptions. An exception is Blegvad (1944), who counted 42–44 scales in specimens from the Gulf of Iran and assigned them to *D. acuta*; I have examined these fishes, but all traces of even the scale pockets are now obliterated.

It seems therefore that scale counts are an unreliable character for separating *D. acuta* from *D. elopsooides*. Delsman (1925) came to the same conclusion and found little difference in vertebral counts in a specimen each of *D. acuta* and *D.*

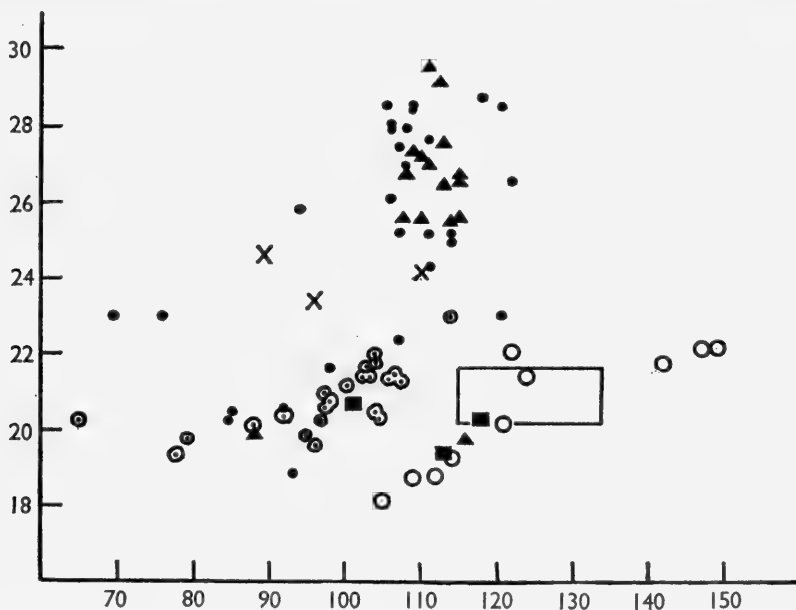


FIG. 1.

Dussumieria acuta. Body depth expressed as a percentage of standard length (ordinate) plotted against standard length in mm. (abscissa) for various populations. Based on specimens (see list of Study Material) labelled or recorded under the following names:

- D. acuta* × Iranian Gulf specimens collected by Blegvad (1944).
 ○ Gulf of Aden specimens
 (in rectangle, five Taiwan specimens, based on Liang, 1948).
 ● All others.
D. elopsooides ■ Hong Kong and China specimens.
 ▲ All others.
D. productissima ○ Specimens from Haifa (eastern Mediterranean).

hasselti (55 and 54 respectively). He also mentions a slight difference in dorsal position, but I have not found this. The weight of other evidence (snout length, body depth, gillraker and dorsal fin ray counts) strongly suggests that the number of scales conforms to the general geographical trends shared by both *D. acuta* and *D. elopsoidea*. On the basis of the four characters mentioned, it is impossible to recognize *D. elopsoidea* as a separate species; the evidence for this is presented below under each heading.

(a) *Body Depth*

The measurements plotted in Text-fig. 1 (as percentages of standard length) refer to specimens of *Dussumieria* covering almost the entire geographical range of the genus. The Aden specimens (open circles) suggest positive allometry with standard length, and this may explain some of the lower figures for the fishes labelled *D. acuta* (black dots). The scatter-diagram shows clearly that size for size, the specimens of *D. elopsoidea* (triangles) cannot be distinguished from *D. acuta* in this character, except in a few cases; three of these are from China (black squares), one is from Amboina, and one bears no locality label. In addition, measurements for five fishes from the Pescadores Islands, Taiwan (*D. acuta* of Liang, 1948) have been placed within a rectangle. The result is a striking similarity between the far-eastern specimens (*D. elopsoidea*) and the Gulf of Aden specimens, with the Mediterranean specimens (encircled dots) also giving low values.

I conclude that body depth cannot be used to separate *D. elopsoidea* from *D. acuta* and that in general the lowest values are found in both the eastern and the western populations, with higher values in intermediate areas. The two specimens recorded (as *D. hasselti*) by Schultz & Wellander (1953) from Batavia appear to be much more slender than any I have measured, having a body depth of only 15% of standard length. In addition, these authors count 61 scale pockets. Unfortunately the fishes were rather damaged, so it would be unwise to include these figures until more specimens can be examined.

(b) *Snout Length*

Although the snout comprises only 8–10% of standard length and variations in its length are barely perceptible, nonetheless, when plotted in a series of histograms for various populations (Text-fig. 2) the results are very suggestive of a cline which may reverse direction after reaching a minimum value in the Indian Ocean. Thus the highest figures are those for specimens from the Gulf of Aden, from the eastern Mediterranean (derivatives of a Red Sea population) and from China; the lowest are those from the coasts of India. The samples are small, but the overall picture deserves attention because of its almost perfect correspondence with the situation found in gillraker counts (Text-fig. 3).

In Text-fig. 2 specimens from each locality have been separated into the species under which they were recorded or labelled. The result shows clearly that in areas where both *D. acuta* and *D. elopsoidea* are represented, there is nothing to distinguish the two, and that *D. elopsoidea* from China, and *D. productissima* from the Mediterranean merely continue the trends already shown by the other populations. Snout

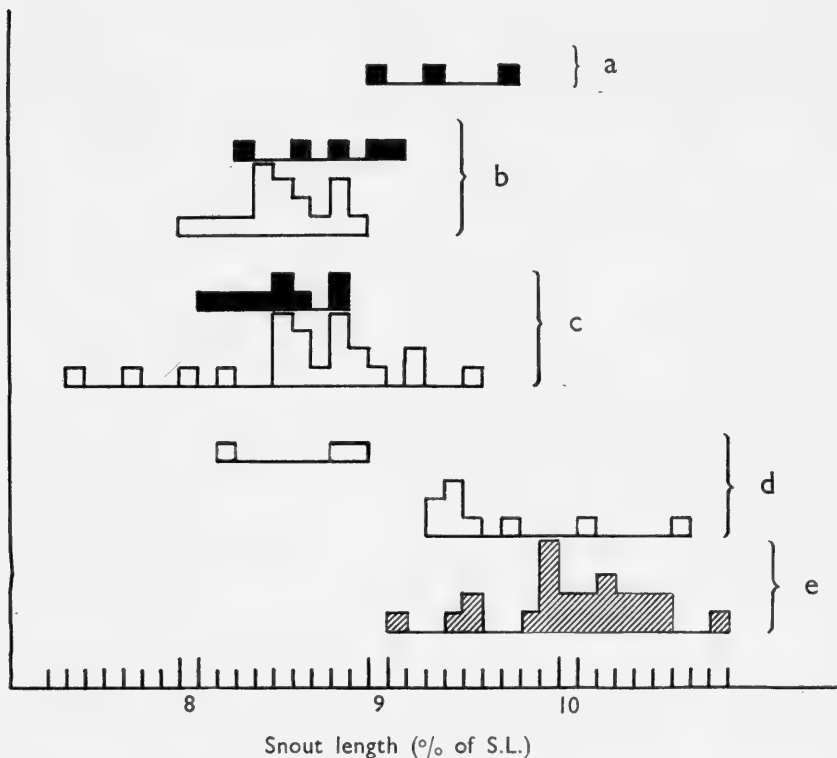


FIG. 2.

Dussumieria acuta. Snout length (expressed as a percentage of standard length) in various populations, showing relative frequency in each group. Based on specimens (see list of Study Material) which have been labelled or recorded under the following names:

White *D. acuta*, Black *D. elopsoides*, Hatched *D. productissima*.

- a. Hong Kong, Foochow, Amoy.
- b. Siam, Amboina, Java, Madura, Sumatra, Borneo, Andamans, Singapore.
- c. Malabar, Calicut, Bombay, Madras, Coromandel.
- d. Gulf of Iran (upper), Gulf of Aden (lower).
- e. Haifa (eastern Mediterranean).

length cannot serve as a basis for distinguishing the species when specimens from the entire range are considered.

(c) Gillrakers

Gillraker frequency counts are presented similarly in Text-fig. 3. These counts were made on the lower part of the first arch only, and included in the count was the occasional raker lying exactly in the angle of the arch. Counts for the Mediterranean specimens lie in the lower part of the range cited by Chabanaud (1933) for *D. productissima*. It is possible that, like other meristic characters, gillrakers are susceptible to exogenous factors (especially temperature), and that a higher count may

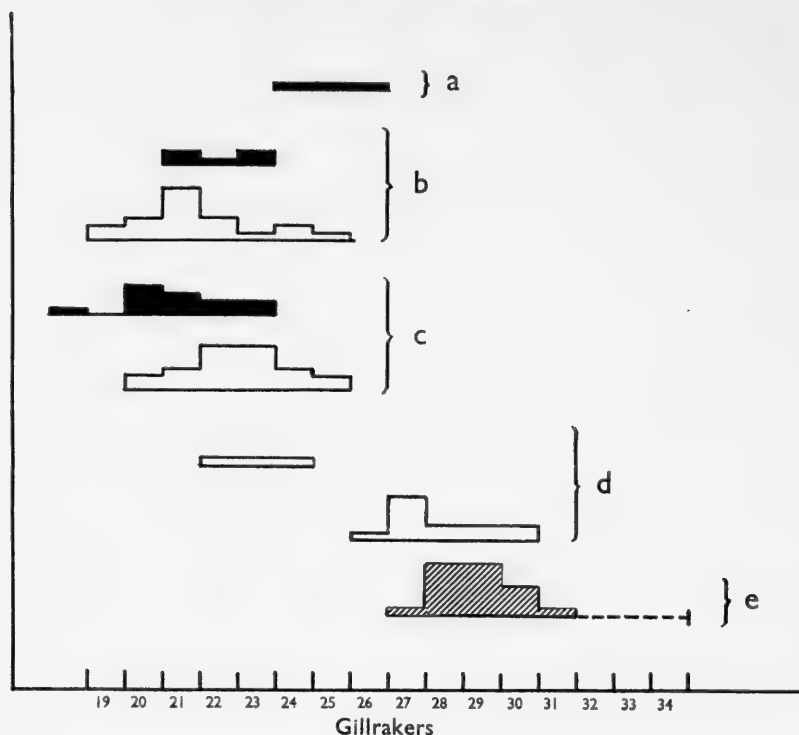


FIG. 3.

Dussumieria acuta. Gillraker count frequencies (lower half of first arch only) in various populations. Based on specimens (see list of Study Material) which have been labelled or recorded under the following names:

White *D. acuta*, Black *D. elopsoides*, Hatched *D. productissima*.

- a. Hong Kong, Foochow, Amoy.
- b. Siam, Amboina, Java, Madura, Sumatra, Borneo, Andamans, Singapore.
- c. Malabar, Calicut, Bombay, Madras, Coromandel.
- d. Gulf of Iran (upper), Gulf of Aden (lower).
- e. Haifa—eastern Mediterranean (broken line includes range given by Chabanaud (1933) for 16 specimens from the Gulf and Isthmus of Suez).

occur in Red Sea populations; this is, however, the reverse of the usual direction in temperature-influenced meristic variations.

As in snout length and body depth, there is a hint that the general west to east trend of decreasing gillrakers is reversed, so that the China specimens again approach the western population in numbers.

The Gulf of Aden specimens (Text-fig. 3d—lower histogram) effectively bridge the gap between "*D. productissima*" (*sensu* Chabanaud) and the remaining populations of *D. acuta*. The sample from the Gulf of Iran (d—upper histogram) only contained three fishes, but a larger sample might well provide a more effective bridge linking the Gulf of Aden population with that of the Indian Ocean. But for the Gulf of Aden specimens, there would be good reason to suppose the Red Sea

D. productissima a distinct species. If a subspecies were considered, then the Gulf of Aden fishes should be included also, but I do not think such a subspecies could be maintained once adequate collections have been made in the western Indian Ocean.

(d) *Dorsal Rays*

The first simple ray of both dorsal and anal fins is easily missed, being small, often minute. For this reason simple and branched rays in both fins have been counted separately, and only the latter plotted in Text-fig. 4. Here the trend, if such there is, appears to be reversed, highest values occurring in Indian Ocean populations, and lowest values at the extremities of the geographical range. But variations in both dorsal and anal rays are very small, and the graph probably shows no more than that once again no distinction can be made between *D. acuta* and *D. elopsoides*.

I have been unable to find other characters on which populations of *Dussumieria* can be distinguished. The shape of the exposed portion of the suboperculum varies somewhat, from a rectangle with an obliquely truncated posterior margin, to a more triangular area with a rather rounded margin (as in *Etrumeus*), but such differences appear to be individual variants. Similarly, the area and shape of the palatopterygoid toothpad also shows some variation, and the size and number of jaw teeth varies. Nor can any distinction be made on the sculpture patterns on the wedge-shaped fronto-parietal surface, the shape of the operculum, or in any body proportions.

Thus the only difference remaining between the three recognized species is in numbers of scales in lateral series, a badly recorded and uncertain character. From the evidence presented on other characters it seems unlikely that scale numbers would in fact show the clear-cut differences suggested by previous descriptions. Therefore, I do not think that three separate species of *Dussumieria* can be maintained, the populations from one area merging imperceptibly with those of the next. There are more grounds for considering the Red Sea population a distinct subspecies, but here again no definite limits can be drawn between the Red Sea specimens and those for example from the Gulf of Aden. If the Red Sea form is to be separated, so also should the far eastern populations, but the latter could only be defined in terms which could include the Red Sea fishes, which would surely be an unrealistic use of the concept of subspecies. It seems preferable therefore, to leave all in one rather variable species, *D. acuta*, until much more work has been done.

Several authors have noted the similarity between specimens of *Dussumieria* from the extreme eastern and western limits of its range. Bertin (1943) suggested "segregation centrifuge". Certainly there is no hydrological similarity between the two areas, so that exogenous factors cannot be held entirely responsible for the reversal in the east-west trend in certain characters.

Finally, mention must be made of *Etrumeus* (*Montalbania*) *albulina* Fowler, which is here placed in the synonymy of *D. acuta*. Bertin (1943) raised this form to generic status, apparently believing it to be intermediate between *Dussumieria* and *Etrumeus*, but nearer to the former than the latter. From Fowler's description and figure however, it is clear that this form cannot be referred to *Etrumeus*. Thus the almost

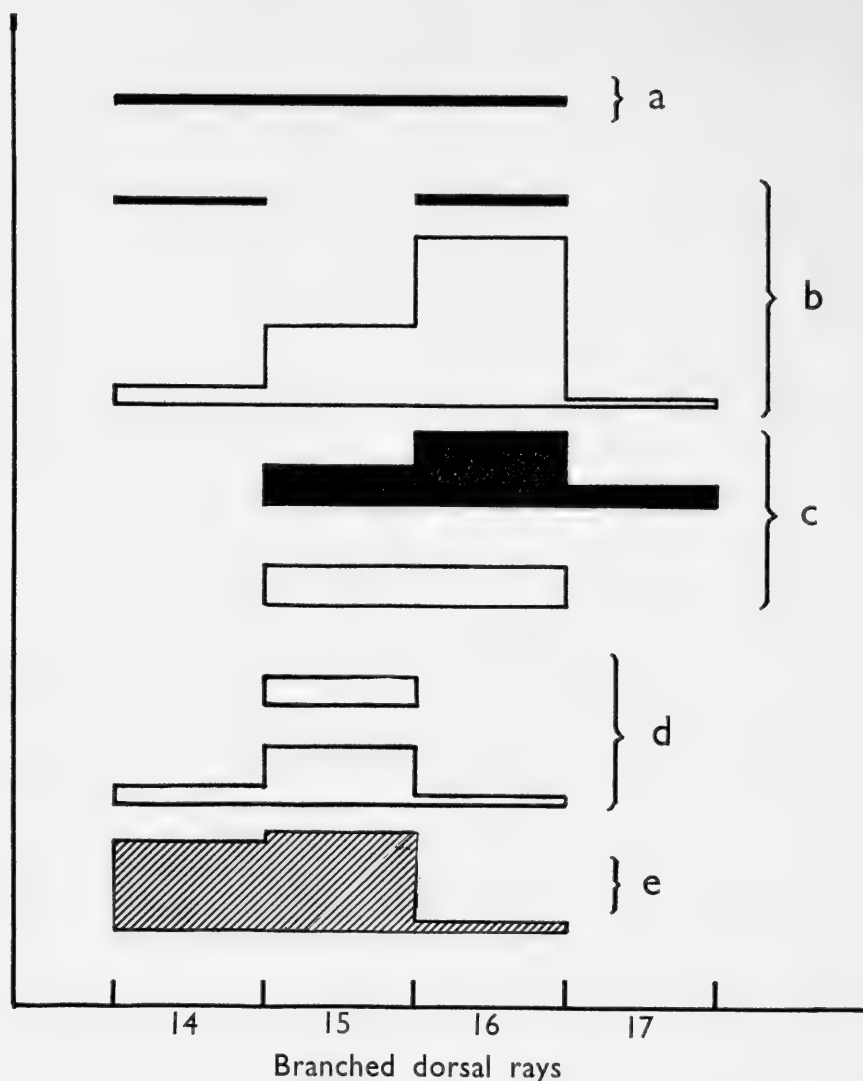


FIG. 4.

Dussumieria acuta. Dorsal finray count frequencies (branched rays only) in various populations, showing relative frequency in each group. Based on specimens (see list of Study Material) which have been labelled or recorded under the following names:

White *D. acuta*, Black *D. elopsoidea*, Hatched *D. productissima*.

- Hong Kong, Foochow, Amoy.
- Siam, Amboina, Java, Madura, Sumatra, Borneo, Andamans, Singapore.
- Malabar, Calicut, Bombay, Madras, Coromandel.
- Gulf of Iran (upper), Gulf of Aden (lower).
- Haifa (eastern Mediterranean).

horizontal border of the operculum, and the shape of the sub-operculum are characteristic of *Dussumieria* (see Text-fig. 30a and b). In no case has a specimen of *Etrumeus* been found with 11 branched anal rays (7-8, Text-fig. 6) or 25 gillrakers (27-36, see Text-fig. 8) or a body depth exceeding 21% of standard length (Text-fig. 9), whereas these are all within the normal range of *Dussumieria*. Bertin (*loc. cit.*) stresses the rather advanced dorsal origin in his *Montalbiana albulina*, but this may be an error; it is not apparent in Fowler's figure. *M. albulina* should therefore be included in *D. acuta*.



FIG. 5.

Dussumieria acuta (from a specimen 148 mm. standard length, Gulf of Aden. Scales omitted).

DESCRIPTION: Based on the holotypes of *D. elopsoides* (124 mm.) and *D. hasselti* (134 mm.); eight fishes, 112-117 mm. standard length from Calicut, S. Malabar; and six fishes, 121-148 mm. standard length from Shihr and Burum, Gulf of Aden. In addition, meristic counts and proportions of snout and body depth for all specimens listed under Study Material have been used (including sixteen syntypes of *D. acuta*).

In percentages of standard length: body depth 18.2-29.6 (Text-fig. 1), head length 25.7-29.4, snout length 7.4-10.6 (Text-fig. 2), eye diameter 5.3-6.3, post-orbital distance 9.2-10.1, inter-orbital width 5.6-5.8, maxilla length 8.4-9.3, lower jaw length 12.3-12.4, pectoral length 15.8-16.2, pelvic length 8.6-8.9, pre-dorsal distance 53.0-59.0, pre-pelvic distance 60.0-65.5, pre-anal distance 79.0-81.5 (84.5 in one instance).

Body moderately compressed, more or less rounded ventrally, its depth less or equal to head length. Snout pointed, larger than eye diameter. Lower jaw projects beyond upper. Maxilla shorter than snout, not quite reaching anterior eye border; two supra-maxillae, the posterior about half width of maxilla, not expanded posteriorly. Curved, conical teeth on premaxilla, maxilla (anterior two thirds) and dentary. Post-orbital about equal to snout length. Dorsal origin nearer to caudal base than to snout tip. Pelvic origin below middle or anterior half of dorsal fin, nearer to caudal base than to pectorals.

Dorsal iv 14-17 (Text-fig. 4), pectoral i 11-14, pelvic i 7, anal iii 11-13.

Gillrakers on lower part of first arch 18-34 (Text-fig. 3), longest raker 3.4-3.5% in standard length.

Scales in lateral series 42-56, transverse 11-12.

Vertebrae 53 (1 fish), 54 (4), 55 (1), 56 (4) (ten fishes from Singapore).

Branchiostegal rays 14-16.

SYNTYPES. Coast of Coromandel (India). Paris Museum, No. 3697, 3694 and 3217.

COLOUR IN ALCOHOL. Dorsal surfaces brown, sides yellow-brown or silver. Tip of snout strongly pigmented. Sometimes a dusky line from operculum to caudal base. Fins pale, but first pectoral ray and tips of caudal dusky.

MAXIMUM SIZE. 216 mm. (Day).

DISTRIBUTION. Red Sea, Madagascar to northern part of Indian Ocean, Indo-Malayan Archipelago and northwards to Hong Kong.

The presence of *D. acuta* in the Mediterranean was first noted by Lissner (1949), and later Ben-Tuvia (1953) stated that these round herrings were common along the shores of Israel and were caught by trawl or purse seine. It will be interesting to see whether the change in environment will produce any corresponding departure from the Red Sea form. Fowler & Steinitz (1955) placed Lissner's five fishes in *D. acuta* (rather than *D. productissima*, as Ben-Tuvia had done for his own specimens), but it is not clear from the text whether this determination was based solely on an approximate scale count, or whether gillrakers, etc. were also considered.

ETRUMEUS Bleeker

Etrumeus Bleeker, 1853, *Verh. Bat. Gen.*, **25** : 48 (Type : *Clupea micropus* Schlegel).

Perkinsia Eigenmann, 1891, *Amer. Nat. Philad.*, **25** : 153 (Type : *Perkinsia othonops* Eigenmann).

Halecula Jordan, 1925, *Stanford Univ. Publ. Biol. Sci.*, **4** : 41 (Type : *Halecula acuminata* Jordan).

Parahalecula Fowler, 1958, *Notul. Naturae, Philad.*, No. 310 : 5. (*Halecula* Jordan, 1925, pre-occupied).

For notes on this synonymy, see under species.

DESCRIPTION. Body elongate, almost round, scarcely compressed. Snout pointed, jaws equal or lower projecting slightly. A single supra-maxilla, about half length of maxilla, tapering uniformly to point anteriorly and about a quarter as deep as maxilla (Text-fig. 28). Maxilla thickened along whole dorsal edge and bearing a branched sensory canal. Small conical teeth along almost entire ventral edge of maxilla. Premaxilla toothed. A w-shaped scute surrounding base of pelvic fins and a smaller, triangular scute immediately behind this. Dorsal 17-22, anal 10-11, 26-39 gillrakers on lower part of first arch. Branchiostegal rays 14-15. Vertebrae 48-56. Anal well behind dorsal, whose origin is a little nearer to snout than to caudal base. Pelvic origin behind dorsal fin. Very small or no fleshy eminence at postero-ventral angle of gill opening (Text-fig. 30a). Ventral margin of operculum rises at steep angle ; exposed portion of suboperculum triangular.

There are five principal populations of *Etrumeus* in temperate seas : North American Atlantic and North American Pacific coasts, the coasts of Japan, of South Africa and of southern Australia. In addition there appears to be a population in the Red Sea, members of which have now colonized parts of the eastern Mediterranean ; another population in the region of the Galapagos Islands ; and a population near Hawaii. This distribution will be discussed later.

Etrumeus teres (DeKay)

(Text-fig. 11)

- Alosa teres* De Kay, 1842, *Nat. Hist. New York*, pt. 4—*Fishes*: 262, pl. 40, fig. 128 (type locality New York region).
- Clupea micropus* Schlegel, 1846, *Faun. Japon. Poiss.*, pts. 10–14: 236, pl. 107, fig. 2 (type locality, southeast coast of Japan).
- Etrumeus micropus* Bleeker, 1853, *Verh. Bat. Gen.*, 25: 48; *Idem*, *op. cit.*, 26: 5; Günther, 1868, *Cat. Fish. Brit. Mus.*, 7: 467; Jordan and Evermann, 1905, *Bull. U.S. Fish Comm.*, 23 (1): 58; Jordan and Herre, 1906, *Proc. U.S. nat. Mus.*, 31: 628; Gilchrist and Thompson, 1917, *Ann. Durban Mus.*, 1 (4): 295; Barnard, 1925, *Ann. S. Afr. Mus.*, 21 (1): 108; Fowler, 1928, *Mem. Bernice P. Bishop Mus.*, 10: 29; *Idem*, 1934, *Proc. Acad. nat. Sci. Philad.*, 86: 410; *Idem*, 1941, *Bull. U.S. nat. Mus.*, No. 100: 576; Chapman, 1948, *Proc. Calif. Acad. Sci.*, 26 (2): 25, figs. 1–3, 7–10, 12–13, 15, 17–18; Svetovidov, 1952, *Tabl. Anal. Faune U.R.S.S. N.S. No. 48*, 2 (1): 102; Smith, 1955, *Ann. Mag. nat. Hist.*, (12) 8: 307; Fowler and Steinitz, 1956, *Bull. Res. Council. Israel*, 5 B (3–4): 261; Matsubara and Iwai, 1959, *Fishes. biol. Res. Jap. Antarct. res. Exped.*, No. 9.
- Harengula teres* Girard, 1859, *Proc. Acad. nat. Sci. Philad.*, 2: 158.
- Dussumieria teres* Brevoort, 1856, in Perry, *Narrative of the U.S. Exped. to Japan*: Washington, 2: 279; Gill, 1861, *Proc. Acad. nat. Sci. Philad.*, 12: 21.
- Etrumeus teres* Günther, 1868, *Cat. Fish. Brit. Mus.*, 7: 467; Jordan and Gilbert, 1882, *Bull. U.S. nat. Mus. Wash.*, 16: 263.
- Etrumeus jacksoniensis* Macleay, 1879, *Proc. Linn. Soc. N.S.W.*, 3: 36, pl. 4, fig. 1; Ogilby, 1886, *Cat. Fishes New South Wales*: 56; McCulloch, 1914, *Rec. W. Aust. Mus.*, 1: 211, pl. 29; Waite, 1921, *Rec. S. Aust. Mus.*, 2 (1): 36, fig. 51; Blackburn, 1941, *Bull. Coun. sci. industr. Res. Aust.*, No. 138: 64.
- Etrumeus sadina* Jordan and Evermann, 1896, *Bull. U.S. nat. Mus. Wash.*, No. 47: 420; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853: 9, fig. 4.
- Etrumeus acuminatus* Gilbert, 1891, *Proc. U.S. nat. Mus. Wash.*, 13: 56.
- Jenkinsia acuminata* Jordan and Evermann, 1896, *Bull. U.S. nat. Mus. Wash.*, No. 47: 419.
- Perkinsia othonops* Eigenmann, 1891, *Amer. Nat. Philad.*, 25: 153; Jordan and Evermann, 1896, *Bull. U.S. nat. Mus. Wash.*, No. 47: 420; Breder, 1928, *Bull. Bingham. oceanogr. Coll. N.Y.*, 2 (2): 5, figs. 2–4; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853: 13.
- Halecula acuminata* Jordan, 1925, *Stanford Univ. Publ. Biol. Sci.*, 4: 41; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853: 24.
- Parahalecula acuminata* Fowler, 1958, *Notul. Naturae, Philad.*, No. 310: 5.
- Stolephorus delicatulus* Seale, 1940, *Reps. Allan Hancock Pacific Exped.* 1932–38, 9: 3.
- Etrumeus othonops* Phillips, 1961, *Calif. Fish Game*, 37: 512.

Notes on Synonymy

Bertin (1943) gave *Clupea sadina* Mitchill 1814 as the earliest name for this species, but in fact he cited a paper published in 1815; it was first used by Mitchill in 1814 in a short paper entitled "Report in part of Samuel L. Mitchill, M.D., Professor of Natural History, &c., on the fishes of New York" (pp. i–x, 1–30). Described by Bashford Dean as "one of the rarest of American contributions to ichthyology", it was reprinted in 1898 by Theodore Gill. In his first description of *Clupea sadina*, Mitchill follows a colour description with "scales fall off very readily; body has a taper, slender, and very delicate appearance. Abdomen not at all serrated, but quite smooth . . .". Although this description fits a species of *Etrumeus*, Mitchill enlarged on it in a paper read within the space of a year (8th December,

1814) and published in 1815, and while this second description of *Clupea sadina* does not contradict the first in any way, it adds details which cannot be reconciled with a species of *Etrumeus*. Thus he places *Clupea sadina*, the "New York Shadine", under a subheading "Bellies carinated without serrae" and says that "On account of the even connection of the false ribs, the belly is not at all serrated, but quite smooth." More important are the discrepancies in meristic counts, and especially that for branchiostegal rays; he counts 7 rays, as against 14 or 15 in *Etrumeus*. He records 9 pelvic rays (normally 8 in *Etrumeus*), and 15 anal rays (never more than 11 counting the minute first, unbranched ray). He also states that the mouth is wide and toothless and mentions "a small smutty spot behind the gill-cover". Finally, he states that there is "A semitransparent space in front of the eyes from side to side."

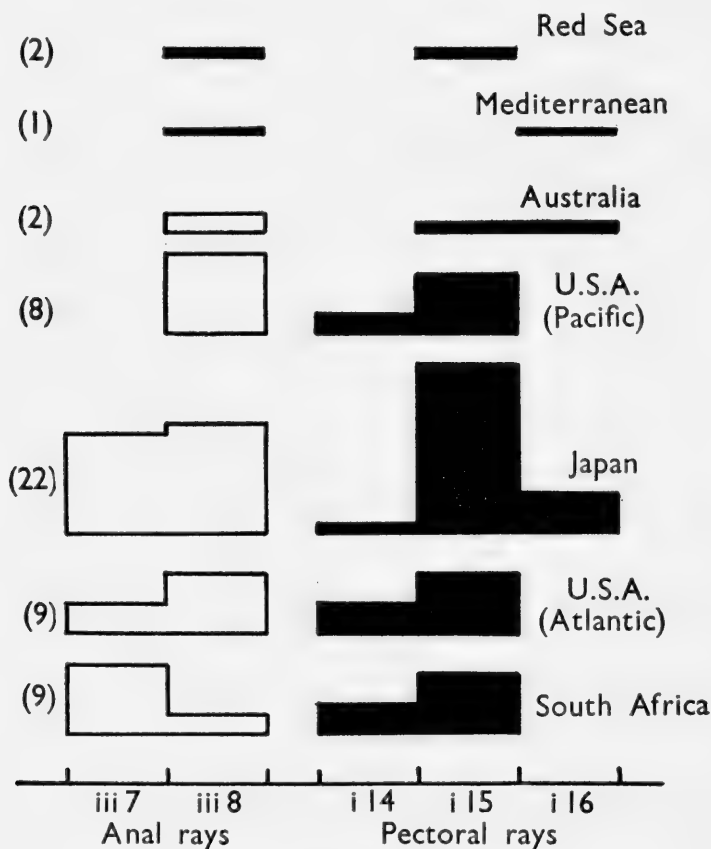


FIG. 6.

Anal (white) and pectoral (black) finray count frequencies in seven different populations of *Etrumeus*. Branched rays only. Number in sample placed in parentheses.

Elsewhere (Whitehead, in press) I have dealt more fully with this problem and have shown that *Clupea sadina* Mitchill need not become a *nomen dubium*, because the second description strongly suggests that Mitchill was describing a species of *Sardinella* and nothing in the first description contradicts this. There is also good reason to believe that both descriptions were based on the same specimen or specimens. DeKay's description of *Etrumeus teres* on the other hand leaves no doubt that it is a species of *Etrumeus*.

Perkinsia othonops (American Pacific) is placed in the synonymy because the corselet of scales surrounding the pectoral fin base, a supposed generic character, is in fact found in large specimens of *Etrumeus*.

Etrumeus (*Montalbania*) *albulina* Fowler has here been synonymized with *Dussumieria acuta* (see p. 312). The advanced pelvic base and the shape of the suboperculum exclude it from *Etrumeus*, and numbers of gillrakers and anal rays are those of *Dussumieria*.

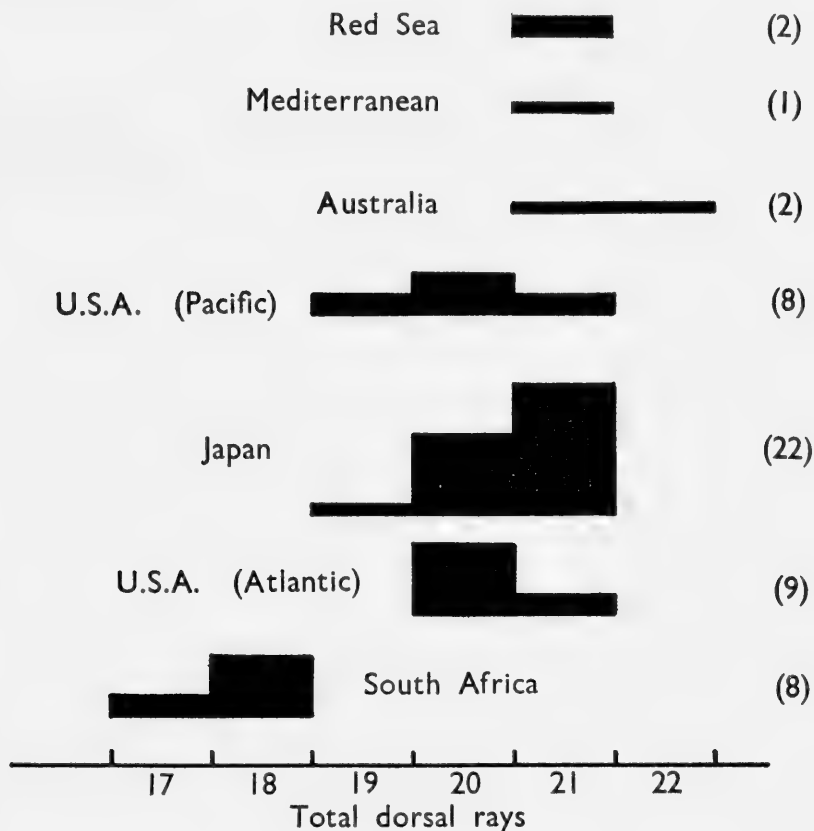


FIG. 7.

Dorsal finray frequencies (branched and unbranched combined) in specimens of *Etrumeus* from seven different populations. Number in sample placed in parentheses.

Halecula acuminata is placed in the synonymy since it was based on juvenile specimens of *E. acuminatus* (Hubbs, *in. litt.*).

(a) *Meristic Differences*

Variations in anal finray counts (Text-fig. 6) are small (7 or 8 branched rays and always 3 simple rays, the first very small and easily missed). Pectoral finray numbers also vary little, and in my material only the Australian, Mediterranean, and Japanese specimens occasionally have 16 branched rays, the remainder 14 or 15 (Text-fig. 6). Differences in dorsal rays are more marked. Normally there are 4 simple rays (occasionally 5), the first very small, but sometimes the last of the simple rays is branched, although recognizable by its length. In dorsal ray numbers one population, that of South Africa, can be separated immediately because of its low count, but the remainder overlap and cannot be separated from each other (Text-fig. 7). Pelvic counts are always 17.

In numbers of gillrakers there is also some variation. The Australian and American Pacific specimens have low counts, the South African are intermediate, and the Japanese, Mediterranean and American Atlantic have high counts (Text-fig. 8.) Again there is considerable overlap between the regions.

(b) *Morphometric Differences*

The most obvious proportional difference found between the samples is that of body depth (Text-fig. 9). Again the Japanese and the American Atlantic specimens resemble each other, and are more slender than the rest. But although insufficient numbers have been measured, Text-fig. 10 strongly suggests that body depth shows positive allometry with standard length. Thus the Japanese form may well be deeper-bodied in larger fishes, as is suggested by the two large Japanese specimens examined (126 and 136 mm.). Certainly the American Atlantic and the American Pacific specimens can be distinguished on this character, but the remainder, and probably also the Japanese specimens, are very similar.

A second morphometric difference is found in the positions of the dorsal, pelvic and anal fins. In the American Pacific specimens these fins are all set slightly further from the snout than in the fishes from the American Atlantic (see Table II). The remaining differences are small and would probably disappear in larger samples.

If the American Atlantic population is taken as the starting point, then the American Pacific fishes can be distinguished by their deeper bodies and fewer gillrakers (27-33; cf. 34-36). The South African population can be separated from all others by its lower dorsal count (17-18 total rays; cf. 19-22). The Japanese population, however, cannot, on the basis of my material, be adequately separated from the American Atlantic population, and the two Australian specimens are in all characters within the range of the American Pacific population.

The distribution of *Etrumeus* is difficult to explain in zoogeographical terms. In some ways it resembles that of *Sardinops* in the Southern Hemisphere, but so far no specimens have been recorded from South American localities; the Galapagos population may represent a southern American form, pushed northwards by the

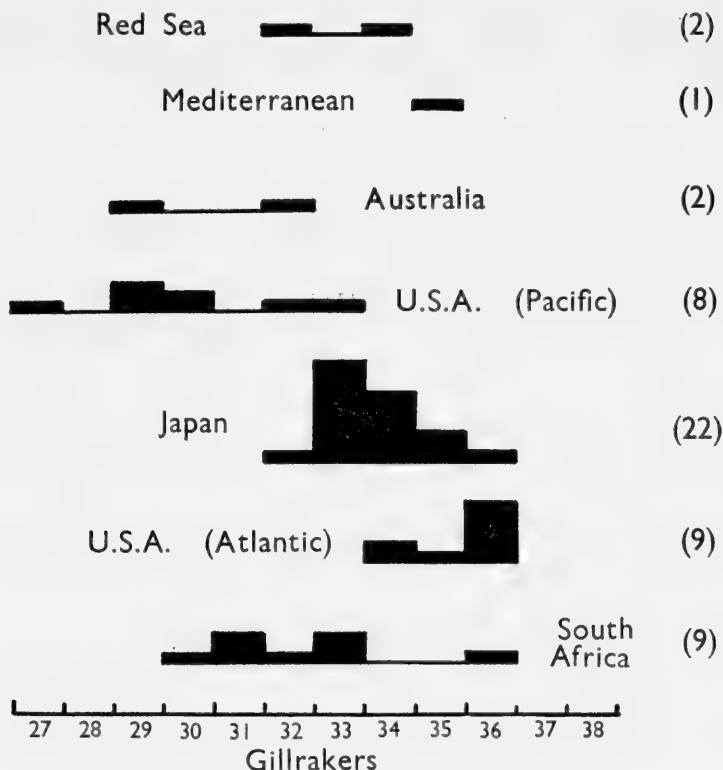


FIG. 8.

Range and frequency in numbers of gillrakers in seven different populations of *Etrumeus*. Number in sample placed in parentheses.

cold Peruvian current. I have not been able to examine specimens from the Galapagos Islands, and cannot relate them to any of the other forms examined here. Possibly the Hawaiian population represents a link between the former and the Japanese population; Jordan & Evermann (1905) stated that their Hawaiian specimens were indistinguishable from the Japanese form.

The isolated Red Sea population is even more difficult to explain. The two Eilat specimens, and the single fish from the eastern Mediterranean, certainly do not belong to the South African population, their nearest neighbours; they appear to be most closely related to the Japanese fishes. This seems to provide further evidence that meristic characters may coincide in populations which are not closely related geographically. It is certainly strange that a species which elsewhere appears to be limited to between the (approximately) 12° and 20° C. isotherms should appear in the Red Sea, and equally remarkable that it should, under these conditions, show so little divergence from other populations.

The isolation of each of these populations is probably complete and it would be expected that each would have diverged at least slightly. It is possible therefore

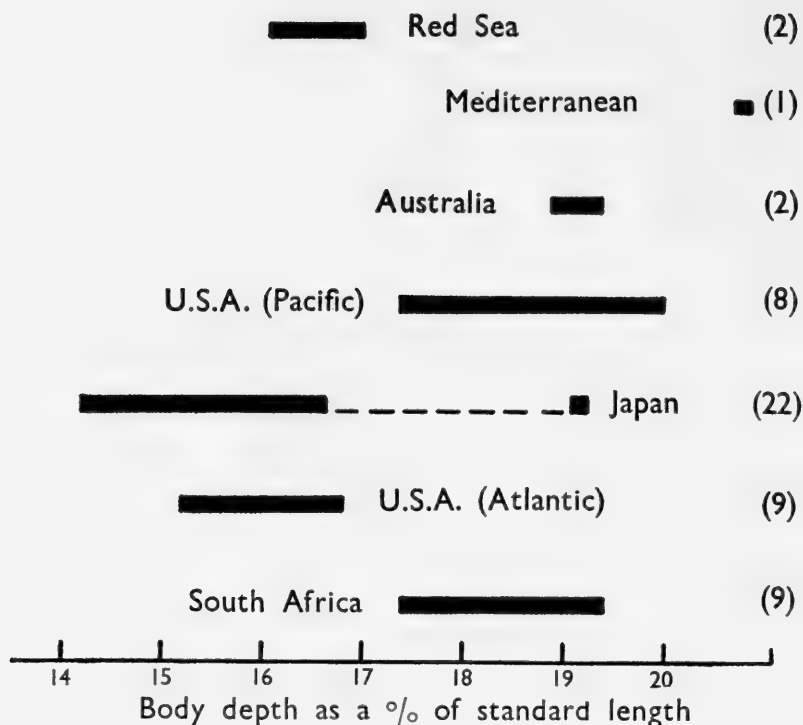


FIG. 9.

Range of variation in body depth (expressed as a percentage of standard length) in seven populations of *Etrumeus*. Number in sample placed in parentheses.

that, since variation is principally restricted to a few meristic characters, similarities have occurred between otherwise well isolated populations purely as a result of parallel evolution. Thus the similarities between the two population pairs cited above may be to a large extent coincidental. This in some ways resembles the case of *Dussumieria* discussed earlier, where morphological similarities contradict probable geographical relationships. But whereas in *Dussumieria* there is a series of both geographical and morphological intermediates, in *Etrumeus* the populations are well isolated.

The genus *Etrumeus* is at present under revision by Prof. Carl L. Hubbs and Mr. Robert Wisner, and I have therefore made no attempt to interpret the present data. I have here followed the example of the last reviewer (Bertin) and have placed all the forms in a single species, rather than create new taxa on the basis of my material alone.

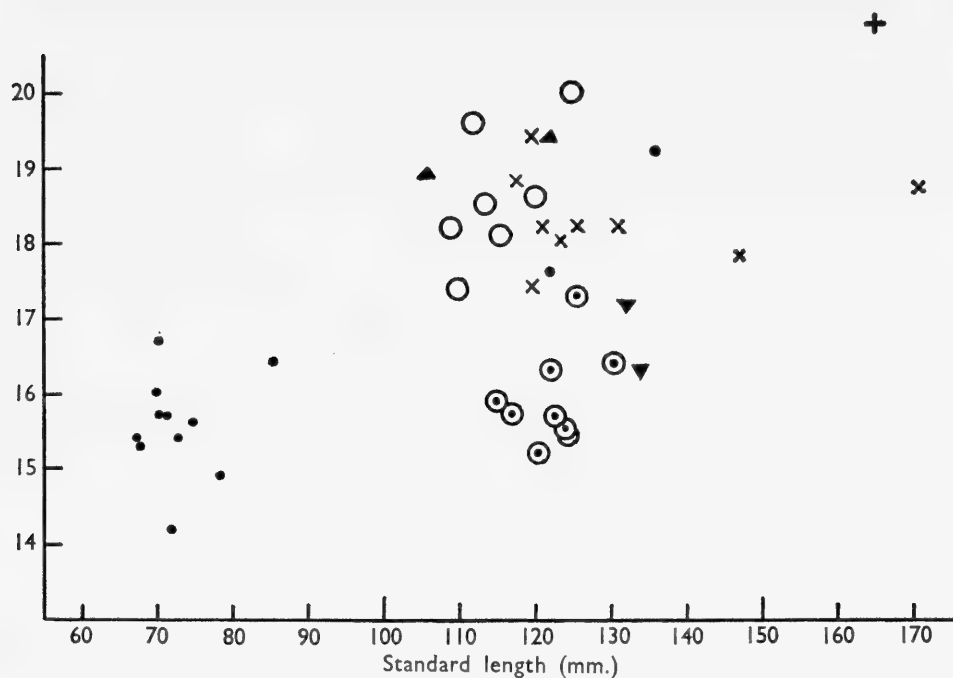


FIG. 10.

Body depth expressed as a percentage of standard length (ordinate) plotted against standard length (abscissa) for specimens of *Etrumeus* from seven different populations.

- Japan and Hong Kong.
- American Atlantic.
- American Pacific.
- × South Africa.
- ▲ Australia.
- + Mediterranean.
- ▼ Eilat (Red Sea).

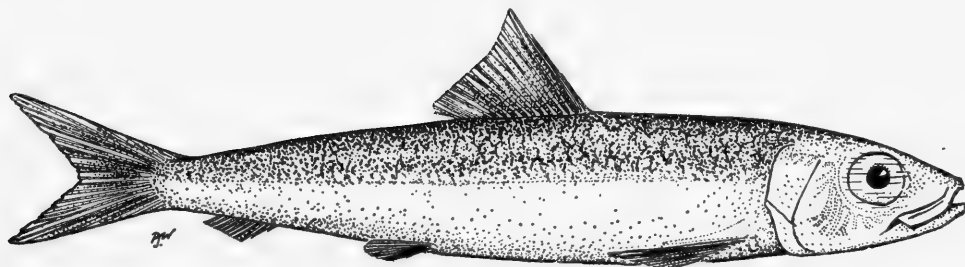


FIG. 11.

Etrumeus teres. From a specimen 150 mm. S.L., ex Woods Hole, Mass. Scales omitted.

***Etrumeus teres* (DeKay)**

(Text-fig. 11)

DESCRIPTION. Based on twelve Japanese specimens (67.5–85.5 mm. standard length); nine fishes from South Africa (117.5–166.0 mm.); two fishes from Australia (105.5–122.0 mm.); nine American Atlantic fishes (115.0–130.2 mm.); seven American Pacific fishes (110.0–125.0 mm.); one Mediterranean fish (165.0 mm.); the type of *Perkinsia othonops* (265.0 mm.); and two Red Sea fishes (133.2 and 134.0 mm.). Specimens listed in Study Material (p. 374).

In percentages of standard length: body depth 14.6–21.2 (Text-figs. 9 and 10), head length 23.2–29.2, snout length 6.9–8.8, eye diameter 7.0–9.8, post-orbital distance 7.9–10.6, maxilla length 8.7–9.7, pectoral length 14.7–17.4, pelvic length 7.6–10.2, pre-dorsal distance 44.0–48.4 (also 49.4 and 50.0), pre-pelvic distance 62.0–70.0, pre-anal distance 82.0–88.0.

Body rounded, little compressed, its depth less than head length. Snout pointed, more or less equal to eye diameter. Lower jaw usually projects beyond upper. Maxilla longer than snout, reaching vertical with anterior border of pupil. A single supra-maxilla, not expanded posteriorly. Conical pointed teeth on pre-maxilla, maxilla and dentary. Post-orbital exceeds snout length. Dorsal origin nearer to snout than to caudal base. Pelvic origin behind dorsal base, nearer to caudal base than to pectorals. Anal origin further from that of pelvics than from anal base.

Dorsal iii–v, usually iv, 14–18, pectoral i 14–16, pelvic i 7, anal iii 7–8 (Text-figs. 6 and 7).

Gillrakers on lower part of first arch 27–36 (Text-fig. 8).

Scales in lateral series 50–56, transverse 13–14 (after Bertin).

Vertebrae 48–56 (Hubbs, *in. litt.*).

Branchiostegal rays 14–15.

COLOUR IN ALCOHOL. Dorsal surfaces light or dark brown, sides silver, the two meeting at a fairly well-defined midlateral line. Tip of snout strongly pigmented. Fins hyaline.

MAXIMUM SIZE. At least 260 mm.

DISTRIBUTION. Seven probably discrete populations: American Atlantic coast (Cape Cod to Gulf of Mexico); American Pacific coast (Gulf of California and north of Los Angeles area—see Phillips, 1951); eastern coast of South Africa (Natal, Zululand); southern coasts of Australia (New South Wales, Victoria, St. Vincent's Gulf, and Albany in Western Australia—see Blackburn, 1941); coasts of Japan (Nagasaki, Wakanoura, Misaki, Aomora, Tokyo); Galapagos Islands (see Seale, 1940); and the eastern Mediterranean (? migrants from the Red Sea), and Red Sea (Eilat) (Fowler & Steinitz, 1956).

Subfamily **SPRATELLOIDINAE***Diagnosis*

Dussumieriid fishes with 6–7 branchiostegal rays, the first three to five attached to the cerato-hyal, which is excavated ventrally (Text-fig. 29). Premaxilla sometimes toothed; maxilla with a broadly expanded posterior supra-maxilla, often as

deep as the maxilla at its widest point ; an anterior supra-maxilla sometimes present. Abdominal scutes represented by either a w-shaped plate surrounding pelvic base (*Spratelloides*, *Jenkinsia*) or a horse-shoe-shaped plate with ascending spines (tribe Ehiravini) (Text-fig. 26) ; exceptionally a series of 6-9 such plates between pectoral and pelvic fins (*Gilchristella aestuarius*), all with ascending spines but never keeled ventrally (Text-fig. 27).

Posterior fontanelles present, but decreasing in extent with size of fish, and in some species (*Ehirava malabaricus*) absent entirely in large fishes. Posterior margin of pre-operculum more or less vertical. Posterior margin of operculum excavated, ventral margin horizontal or slightly inclined. A small, fleshy eminence at postero-ventral angle of gill opening, prominent in some genera. Lower edge of inter-operculum exposed in lateral view. Sub-operculum rectangular.

Dorsal rays 11-16 ; anal 9-20. Transverse scales on body 7-10. Vertebrae 30-46.

Adult size 50-110 mm.

Five genera are recognized here, *Ehirava*, *Gilchristella*, *Sauvagella*, *Spratelloides* and *Jenkinsia*. The first three differ so much from the other two that I have thought it advisable to split the *Spratelloidinae* into two tribes.

- A. Pelvic scute with an ascending, pointed spine ; a single supra-maxilla ; premaxilla toothed ; pelvic fins under anterior half of dorsal or in advance of first dorsal ray ; fleshy eminence at postero-ventral angle of gill opening little developed ; posterior fontanelles broadly divided anteriorly by wedge of bone Ehiravini
- B. Pelvic scute w-shaped as in *Dussumieriinae*, without ascending spine ; one or two supra-maxillae ; pre-maxilla normally edentulous ; pelvic fins under middle, or second half of dorsal ; fleshy eminence at postero-ventral angle of gill opening usually well developed ; posterior fontanelles narrowly divided anteriorly in most species *Spratelloidini*

Notes on Tribe Ehiravini

In his review of the round herrings, Bertin (1943) recognized two genera from southern Africa and Madagascar which differed from *Spratelloides* in having the pelvic base in advance of the dorsal origin, not under the dorsal. The first, *Gilchristella* Fowler, contained *G. aestuarius* Fowler, and also Sauvage's *Spratelloides madagascariensis*, into which Bertin had earlier placed his two subspecies of *Sauvagella madagascariensis* (*longianalis* and *breviodorsalis*, Bertin, 1940). The second genus, the monotypic *Sauvagella* Bertin, was further distinguished by possession of a split anal, the last two anal rays being distinctly separated from the rest of the fin (confirmed in alizarin preparations, Bertin, 1943). Bertin (1943) felt it possible that *Sauvagella bianalis* might be merely a mutant form of *Gilchristella madagascariensis*, the two differing little except in the form of the anal fin.

Later, Angel, Bertin & Guibé (1946) proposed the *nomen novum* *Spratellomorpha* to replace *Sauvagella* of Bertin, 1943 (not of Bertin, 1940, which was now included in *Gilchristella*). This is discussed under the synonymy of *Sauvagella*.

These three South African and Malagasi species could be placed in a single genus but for the discovery that *G. aestuarius*, alone of the whole *Dussumieriidae*, possesses ventral scutes (Whitehead, 1962a). While the split anal fin of *S. bianalis* could

perhaps be considered a chance mutation, the possession of abdominal scutes cannot be lightly dismissed in view of the importance of scutes in the phylogeny of the group as a whole. I have found these scutes in two specimens of *G. aestuarius* from Durban, and also in seven further specimens from various South African localities (see under species description).

Although *G. aestuarius* is thus unique, and shows supra-limital variation (in the sense of Myers, 1960) in this one character, otherwise it closely resembles its non-scuted geographical relatives. Therefore, I do not think *G. aestuarius* should be separated from the South African species at higher than generic level. Nor does it seem that *G. aestuarius* is the sole representative of an ancient line deriving from earlier clupeids. It belongs to a group in which at least one other clupeid character is also found, the divided anal fin of *S. binalis* (i.e. in the clupeid genus *Corica*). It would appear therefore that the Ehiravini share certain potential genetic patterns characteristic of the clupeids, but that these have shown only a partial development in some species but not at all in others. The Ehiravini may thus be derived from forms which lay close to the split between the round herrings and the true herrings.

The South African group, although all more closely allied to *Spratelloides* than to any other dussumierid genus, differ from the latter in six important characters.

- i. Pelvic scute with lateral spines (Text-fig. 26).
- ii. A single supra-maxilla.
- iii. Advanced pelvics.
- iv. Fleshy eminence on postero-ventral angle of cleithrum little developed.
- v. A toothed premaxilla.
- vi. Posterior fontanelles broadly divided by wedge of bone anteriorly, in front of which is a triangular depression (Text-fig. 32a).

These characters are also shared by *Spratelloides malabaricus* from the Malabar coast of India, which should therefore be included with the South African species. *S. malabaricus* is at the same time identical to *Ehirava fluviatilis* Deraniyagala. Deraniyagala (1929) proposed a new family, the Ehiravidae, on the strength of this one species, distinguishing it from the Dussumeriidae by the possession of only one supra-maxilla; he considered *Ehirava* intermediate between *Spratelloides* and *Dussumieria*. Since its description, *Ehirava* has been mentioned only once (Monroe, 1955). Since *S. malabaricus* cannot be retained in *Spratelloides*, the genus *Ehirava* is available for it. At the same time I have been unable to find any but very small differences between *S. malabaricus* and the Malagasi species *Gilchristella madagascariensis*. The latter should therefore be placed in *Ehirava* also, but it can be separated from the Indian form at species level, at least on the available material; the greatest difference is in scale numbers, but this may well prove dependent on locality when a larger sample is examined.

The tribe Ehiravini thus contains three genera and five species.

Tribe EHIRAVINI

Diagnosis

Members of the subfamily Spratelloidinae which possess only a single supra-maxilla and a toothed premaxilla. Eminence on postero-ventral angle of cleithrum

poorly developed and similar to that found in *Etrumeus* or *Dussumieria*. Pelvic scute horse-shoe-shaped, with pointed, ascending spines. Pelvic origin just behind, below, or just in front of dorsal origin. Posterior fontanelles broadly separated at anterior end by wedge of bone (frontals), in front of which is shallow triangular depression.

DISTRIBUTION. Eastern coast of South Africa, coast of Madagascar, and the western coast of India.

KEY TO GENERA

- A. Additional scutes absent between pectoral and pelvic fins
 - i. Anal fin entire, last two rays not separate *Ehirava*
 - ii. Last two anal rays separate from rest of fin *Sauvagella*
- B. Six to nine abdominal scutes between pectoral and pelvic fins ; anal fin entire
Gilchristella

Ehirava Deraniyagala

Ehirava Deraniyagala, 1929, *Spolia Zeylan*, **15** : 34, pl. 14 (type *E. fluviatilis* Deraniyagala = *Spratelloides malabaricus* Day).

Sauvagella Bertin (*part.*), 1940 (*Sauvagella madagascariensis*, i.e. *S. m. longianalis* and *S. m. brevidorsalis*, but non *S. m. bianalis*), *Bull. Mus. Hist. nat. Paris*, (2) **12** : 300 (type *Spratelloides madagascariensis* Sauvage ex Madagascar) ;

DESCRIPTION. Body elongate, more compressed than in *Spratelloides*, snout pointed, lower jaw projecting. Posterior supra-maxilla present, as deep as maxilla, anterior absent ; maxilla toothed, with anteriorly indented lower border (Text-fig. 28f). Premaxilla toothed. Small fleshy eminence on postero-ventral angle of cleithrum (cleithral flap), not more prominent than in *Dussumieria* (Text-fig. 30b). Posterior border of operculum slightly indented, but not to the extent found in *Spratelloides* ; junction between operculum and sub-operculum not horizontal (as in *Spratelloides*, Text-fig. 30c), but inclined (as in *Dussumieria*, Text-fig. 30b).

A single (pelvic) scute with ascending spines (Text-fig. 26). Pelvic origin just behind or in front of dorsal origin. Branchiostegal rays 6. Scales not strongly deciduous.

Two species recognized, but more material may merge the differences shown here.

- a. Snout equal to or smaller than eye ; pelvic origin below first dorsal or slightly behind ; scales 35-38 *E. malabaricus*
- b. Snout a little greater than eye ; pelvic origin in front of first dorsal ray ; scales 43-48
E. madagascariensis

Ehirava malabaricus (Day)

(Text-fig. 12)

Spratelloides malabaricus Day, 1873, *Proc. zool. Soc. Lond.*, 240 ; *Idem*, 1878, *The Fishes of India* : 648, pl. 161, fig. 5 (Type locality : Malabar, India) ; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 17.

Ehirava fluviatilis Deraniyagala, 1929, *Spolia Zeylan*, **15** : 35, pl. 14 (Type locality : Ceylon) ; Monroe, 1955, *Marine and freshwater fish. Ceylon* : 28.

Note on Synonymy

The five specimens of *S. malabaricus* in the Museum are identical to the type and paratypes of *E. fluviatilis* in both meristic characters and proportional measurements.

Pellonulops Smith, purported to be based on *Spratelloides madagascariensis* Sauvage, is not placed in the synonymy because the genus is clearly based in fact on a clupeid, not a dussumieriid. Thus Smith (1949) described both pre- and post-pelvic scutes, and the presence of the latter eliminates the chance that his specimens were *Gilchristella aestuarius*.

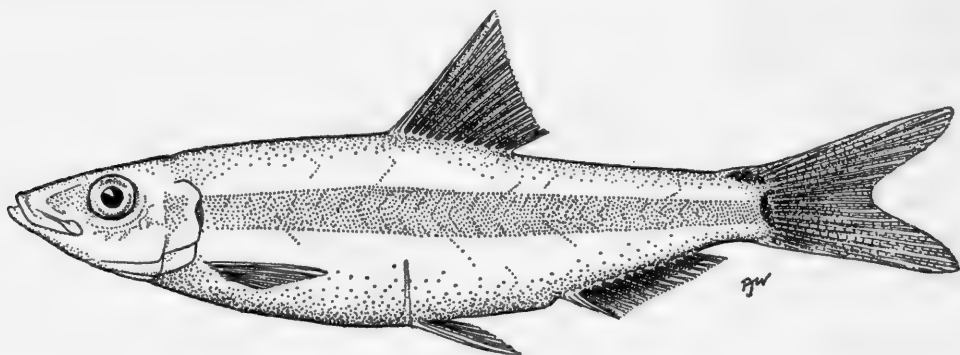


FIG. 12.

Ehirava malabaricus. From a specimen 58 mm. standard length, Canara. Scales omitted.

DESCRIPTION. Based on the type and seven of the larger paratypes of *E. fluviatilis* from Kehelvatta, Ceylon (35.1–48.6 mm. standard length) and five specimens of *S. malabaricus* from Malabar (40.5–56.2 mm.).

In percentages of standard length: body depth 15.4–22.4, head length 22.4–26.7, snout length (5.7 one fish) 6.6–8.2, eye diameter 6.8–8.5, post-orbital distance 7.9–9.8, maxilla length 8.7–9.9, pectoral length 13.9–16.3, pelvic length 11.3–12.5, pre-dorsal distance 50.0–52.2, pre-pelvic distance 49.1–52.5 (53.4), pre-anal distance 72.0–76.5 (80.0).

Body fairly strongly compressed, especially in larger fishes, depth less than head length. Snout pointed, equal or a little smaller than eye. Jaws unequal, lower projecting. Maxilla longer than snout, almost reaching vertical with anterior rim of pupil, with excavated lower edge anteriorly (Text-fig. 28f). One supra-maxilla only, expanded posteriorly as in *Spratelloides*. Maxilla with a single row of conical teeth along lower edge. Pre-maxilla also with conical pointed teeth in a single series.

Dorsal origin mid-way between snout and caudal base. Pelvic origin below first dorsal ray or just behind, a little nearer anal origin than to pectoral base. Anal origin almost equidistant between that of pelvics and caudal base.

Dorsal iii 11–12, pectoral i 10–12, pelvic i 7, anal ii–iii 12–15 (total 14–18).

Scales in lateral series 35–38, 9 transverse.

Branchiostegal rays 6.

HOLOTYPE. Kehelvatta, Ceylon. B.M. (N.H.) 1929.7.1.1.

COLOUR IN ALCOHOL. A uniform light brown with in some specimens a faint silvery midlateral stripe not quite as broad as eye. A short oblique line of dark pigment on lower half of caudal base and another, almost horizontal, line along upper edge of caudal base. In smaller specimens, bases of dorsal and anal fins pigmented.

SIZE. Largest specimen examined 56.2 mm. standard length.

ALLOMETRY. Apart from the eye (negative) there is no evidence from the specimens measured that any other body part shows allometry with standard length.

DISTRIBUTION. Ceylon and Malabar coast of India.

Ehirava madagascariensis (Sauvage)

Spratelloides madagascariensis Sauvage, 1883, *Bull. Soc. philom., Paris* (7) 7: 160; *Idem*, 1891, *Hist. Nat. Madagascar, Poiss.*: 496, pl. 48, fig. 2.

Sauvagella madagascariensis longianalis and *S. m. brevidorsalis* Bertin, 1940, *Bull. Mus. Hist. nat., Paris* (2) 12: 300.

Gilchristella madagascariensis Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853: 21; Angel, Bertin and Guibé, 1946, *Bull. Mus. Hist. nat., Paris* (2) 18: 473-4.

DESCRIPTION. Based on a specimen, 40.0 mm. standard length *ex* Madagascar (paratype of *Spratelloides madagascariensis*); and eleven other fishes, 41.0-52.5 mm. from Buffalo river, Cape Province (S. Africa).

In percentages of standard length: body depth 16.0-22.8, head length 25.0-28.2, snout length 7.3-7.8, eye diameter 7.3-8.5, post-orbital (8.2) 10.6-11.9, maxilla length 8.7-9.0, pre-dorsal distance 50.3-56.0, pre-pelvic distance 50.0-54.9, pre-anal distance 66.8-72.5.

Body compressed, depth less than head length. Snout pointed, usually a little greater than eye diameter. Jaws subequal, lower projecting. Maxilla longer than snout, reaching vertical through anterior border of pupil. Maxilla shape as in *Gilchristella*. A single supra-maxilla.

Dorsal origin slightly nearer caudal base than snout. Pelvic origin in front of dorsal, about equidistant between snout and caudal base, nearer anal base than pectoral base. Anal nearer pelvic base than caudal base.

Dorsal iv 10-11, pectoral i 9, pelvic i 7, anal iii 14-17, gillrakers 40-56 (lower numbers mainly in the smaller specimens and vice versa).

Scales in lateral series 43-48, transverse 8.

TYPE. Madagascar. Paris Museum No. 3794.

COLOUR IN ALCOHOL. Uniform grey-brown. A faint silvery mid-lateral stripe. Two pigmented lines at base of caudal, as in *Sauvagella bianalis*.

SIZE. 60 mm. (Bertin, 1943).

DISTRIBUTION. Madagascar and Buffalo river, King Williamstown (Cape Province).

GILCHRISTELLA Fowler

Gilchristella Fowler, 1935, *Proc. Acad. nat. Sci. Philad.*, 87: 365, fig. 4 (Genotype: *Spratelloides aestuarius* Gilchrist from Swartkops river).

DESCRIPTION. Body compressed, more so than in *Ehirava*, its depth almost equal to head length. Snout pointed, lower jaw projecting. Anterior supra-maxilla

absent; posterior supra-maxilla expanded posteriorly to almost depth of maxilla, anterior shaft-like. Maxilla toothed along lower edge; pre-maxilla toothed. Small fleshy eminence on postero-ventral angle of cleithrum scarcely as developed even as in *Ehirava* (i.e. nearer to the *Etrumeus* than to the *Dussumieria* condition). Posterior border of operculum slightly indented, as in *Ehirava*; junction between operculum and suboperculum not horizontal but oblique, more steeply inclined than in *Ehirava* and thus resembling that of *Etrumeus* (Text-fig. 30a).

Pelvic scute with thin, pointed ascending arms. Between pectoral and pelvic bases, a series of six to nine similar scutes (Text-fig. 27).

Dorsal origin a little further from snout than caudal base; pelvic origin below first dorsal ray or in front, equidistant between snout and caudal base. Branchiostegal rays 6-7. Scales moderately deciduous.

A single species recognized here.

Gilchristella aestuarius (Gilchrist)

(Text-fig. 13)

Spratelloides aestuarius Gilchrist, 1914, *Mar. Biol. Rep. S. Afr.*, No. 1: 55 (Type material from: Swartkops river, Port Elizabeth); Regan, 1916, *Ann. Durban Mus.*, 1: 167; Gilchrist and Thompson, 1917, *Ann. Durban Mus.*, 1 (pt. 4): 296; Barnard, 1925, *Ann. S. Afr. Mus.*, 21 (pt. 1): 109.

Gilchristella aestuarius Fowler, 1935, *Proc. Acad. nat. Sci. Philad.*, 87: 365, fig. 4; Bertin, 1943 *Bull. Inst. océanogr. Monaco*, No. 853: 21.

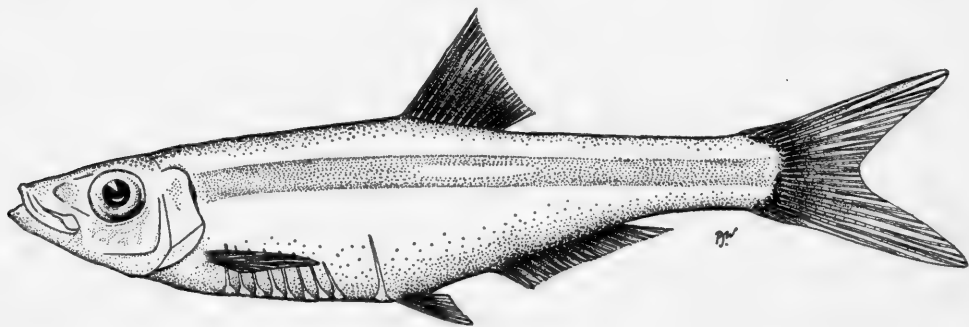


FIG. 13.

Gilchristella aestuarius. From a specimen 60 mm. standard length, Durban. Scales omitted.

DESCRIPTION. Based on two fishes 51.0 and 53.0 mm. standard length from Durban, and seven fishes 35.9-51.5 mm. from other South African localities (East London, Knysa, St. Lucia, Keimouth, Milnerton and the type locality Swartkops river—on loan from Professor J. L. B. Smith).

In percentages of standard length: body depth (17.5 one fish) 19.2-24.5, head length 25.2-27.5, snout length 6.3-7.5 (8.1), eye diameter 6.8-8.1, post-orbital 8.1-9.5, maxilla length 10.2, pectoral length 14.2, pelvic length 11.7, pre-dorsal distance 52.5-57.7, pre-pelvic distance 50.0-54.4, pre-anal distance 66.7-70.0.

Body strongly compressed, especially in larger fishes, its depth just less than head length. Snout pointed, usually a little less than eye diameter. Jaws sub-equal, lower projecting slightly. Maxilla longer than snout, reaching vertical through anterior border of pupil, anterior excavation not as pronounced as in *Ehirava* (see Text-fig. 28f). One supra-maxilla only, shape and proportions as in *Ehirava*. Maxilla and premaxilla with single row of conical teeth.

Dorsal origin a little further from snout than caudal base. Pelvic origin below first dorsal ray or more usually in front, equidistant between snout and caudal base or a little nearer the latter, and nearer to anal than to pectoral base. Anal origin nearer that of pelvics than to caudal base. Six to nine pre-pelvic scutes.

Dorsal iii 11-12, pectoral i 10-11, pelvic i 7, anal iii 17 (total 20).

Scales in lateral series 40, transverse 9-10 (Bertin, 1943).

Branchiostegal rays 6-7, gillrakers on lower part of first arch 39-45; inner series on first two arches absent, and lower part of inner series on third arch also absent.

TYPES. Swartkops river, near Port Elizabeth. South African Museum. (Nos. 10822-4).

COLOUR IN ALCOHOL. A uniform light brown with a faint midlateral silvery band. Individual bases of dorsal and anal rays pigmented (black). Two short dark pigment lines at base of anal, one almost horizontal along upper border, the other oblique on lower border.

SIZE. Largest fish examined 53.5 mm. Barnard (1925) gives maximum size 70 mm.

ALLOMETRY. No indication except with eye measurement (negative allometry with standard length).

DISTRIBUTION. Estuaries and lagoons of the eastern coast of South Africa.

SAUVAGELLA Bertin

Sauvagella (part.) Bertin, 1940 (*Sauvagella madagascariensis bianalis* only), *Bull. Mus. Hist. nat.*

Paris (2) 12: 300; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853: 22.

Spratellomorpha Bertin, 1946, in Angel, Bertin and Guibé, 1946, *Bull. Mus. Hist. nat. Paris* (2)

18: 473-4 (type *Sauvagella madagascariensis bianalis* Bertin ex Madagascar).

Note on Synonymy

Spratellomorpha was proposed (Angel, Bertin & Guibé, 1946) as a *nomen novum* in order to overcome the confusion arising from the splitting of *Spratelloides madagascariensis* into three subspecies (Bertin, 1940), first placed all together in the genus *Sauvagella* and later separated, two being united and placed in *Gilchristella*. Because of this the meaning of *Sauvagella* became obscured. However, as a result of placing *G. madagascariensis* (in the sense of Bertin, 1943) in *Ehirava*, there is no reason why *Sauvagella* cannot again be applied to *bianalis*; thus *Sauvagella* Bertin, 1940 and *Sauvagella* Bertin, 1943 both included *bianalis*, the latter description being the more definitive since the two other subspecies had by that time been transferred to *Gilchristella*.

DESCRIPTION. Body elongate, compressed, as in *Gilchristella*. Snout pointed, lower jaw projecting. Anterior supra-maxilla absent; posterior supra-maxilla

expanded posteriorly to almost maxilla depth, anterior shaft-like. Pre-maxilla and maxilla with a single row of conical teeth. Fleshy eminence on postero-ventral angle of cleithrum very small, similar to that in *Etrumeus* (Text-fig. 30a). Posterior border of operculum slightly excavated; junction between operculum and sub-operculum not as steeply inclined as in *Gilchristella* but resembling that in *Ehirava* and thus *Dussumieria* (Text-fig. 30b).

Pelvic scute with thin, pointed ascending arms. No abdominal scutes.

Dorsal origin further from snout than caudal base. Pelvic origin in front of dorsal.

Branchiostegal rays 6.

A single species.

Sauvagella bianalis Bertin

(Text-fig. 14)

Sauvagella madagascariensis bianalis Bertin, 1940, *Bull. Mus. Hist. nat. Paris*, (2) 12: 300.

Sauvagella bianalis Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853: 22, fig. 8.

Spratellomorpha bianalis Bertin, 1946, in Angel, Bertin and Guibé, 1946, *Bull. Mus. Hist. nat. Paris* (2) 18: 473-4.

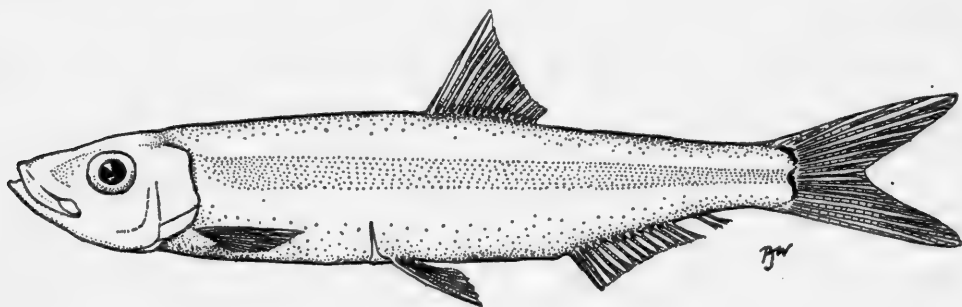


FIG. 14.

Sauvagella bianalis. From a specimen 47 mm. standard length, Madagascar (syntype, Paris Museum No. A 5174). Scales omitted.

DESCRIPTION. Based on four fishes, 44.0-45.5 mm., *ex* Madagascar (types of *Sauvagella bianalis*).

In percentages of standard length: body depth 17.1-18.0, head length 25.2-26.5, snout length 6.9-7.1, eye diameter 7.2-7.8, post-orbital 8.4-8.6, maxilla length 9.7-10.0, pre-dorsal distance 53.4-56.5 (62.8 one fish), pre-pelvic distance 49.4-52.2, pre-anal distance 69.0-72.5.

Body compressed, but body depth less than head length. Snout pointed, a little less than eye diameter. Jaws subequal, lower projecting slightly. Maxilla longer than snout, reaching vertical through anterior border of pupil. Maxilla as in *Gilchristella*. A single supra-maxilla.

Dorsal origin a little nearer caudal base than snout. Pelvic origin in front of dorsal, nearer to anal base than to pectoral base. Anal origin nearer that of pelvics than to caudal.

Dorsal iii 12-13, pectoral i 12, pelvic i 7, anal iii 11-12 + 2.

Last two rays of anal fin separated from others by a gap equal to three rays. After examining an alizarin stained specimen, Bertin (1943, p. 23) stated that the gap between the two parts of the fin is due, not to a complete separation of the two, but the fact that "*l'actiniophore du premier rayon de l'anale postérieure est trois fois plus allongé, dans sa partie horizontale, que les autres actiniophores.*"

Scales in lateral series 42-45, transverse 8-9. Vertebrae 45-46 (16-17 caudal) (after Bertin).

SYNTYPES. Madagascar. Paris Museum No. A.5174.

COLOUR IN ALCOHOL. A uniform grey-brown. A faint silvery midlateral stripe. Caudal base with two dark pigmented lines, as in *Gilchristella aestuarius*.

SIZE. 60 mm. (Bertin, 1943).

ALLOMETRY. Except in eye size (negative) no allometry found in other body parts with standard length.

DISTRIBUTION. Madagascar.

Tribe SPRATELLOIDINI

Diagnosis

Members of the subfamily Spratelloidinae which possess a w-shaped pelvic scute (Text-fig. 25), two supra-maxillae (except in *Jenkinsia*), well-developed posterior fontanelles usually narrowly divided anteriorly, and pelvic fins below the middle of the dorsal.

DISTRIBUTION. Ranging from Japan and Australia to the Red Sea and South Africa, with a genus in the Caribbean area (Venezuela to Bermuda).

Two genera :

- A. Two supra-maxillae; premaxilla edentulous; cleithral flap well developed; posterior border of suboperculum evenly rounded; posterior fontanelles always narrowly divided anteriorly; Indo-pacific region *Spratelloides*
- B. A single supra-maxilla; premaxillary teeth sometimes present; cleithral flap little developed; posterior and ventral margins of suboperculum meeting at well-defined angle; posterior fontanelles sometimes broadly divided anteriorly; Caribbean region *Jenkinsia*

In many ways *Jenkinsia* stands between *Spratelloides* and the genera of the Ehiravini, but the evolution of the spined pelvic scute seems to be such an important step taken by the Ehiravini in the direction of the Clupeidae that *Jenkinsia* must be placed closer to *Spratelloides*. In addition, within the genus *Jenkinsia*, one species differs from *Spratelloides* principally in lacking the anterior supra-maxilla, whereas the other species is much nearer the Ehiravini, possessing premaxillary teeth, and a formation of the posterior fontanelles which differs from that in *Spratelloides*. This is further discussed under the generic descriptions.

Bertin (1943) included the Caribbean species in *Spratelloides*, but the two are well separated by the characters listed in the key above, geographical isolation reinforcing this distinction.

SPRATELLOIDES Bleeker

Spratelloides Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 29 (type *Clupea argyrotaeniata* Bleeker = *Clupea gracilis* Schlegel).

Stolephorus (non Lacépède) Fowler, 1941, *Bull. U.S. nat. Mus.*, **13** (No. 100) : 561.

Note on Synonymy

Some recent authors have substituted *Stolephorus* for Bleeker's *Spratelloides*, but this is quite wrong and is discussed fully after the synonymy for *Spratelloides gracilis*.

DESCRIPTION. Body elongate, slightly compressed, rounded ventrally; snout pointed, jaws equal or lower very slightly projecting. Two supramaxillae, the second (posterior) bone paddle-shaped with a slender anterior shaft; maxilla toothed, with evenly rounded lower border (Text-fig. 28). Pre-maxilla edentulous. Fleshy eminence on postero-ventral angle of cleithrum (cleithral flap) well-developed, indented anteriorly (Text-fig. 30c), gill filaments of first arch also indented to accommodate cleithral flap. Posterior border of operculum strongly indented, more so than in *Ehirava*. Junction between operculum and sub-operculum horizontal, the latter bone subrectangular, its posterior margin rounded. Interoperculum exposed and three or four branchiostegal rays visible externally. Posterior border of pre-operculum vertical. Posterior border of gill opening s-shaped.

Two posterior fontanelles with a narrow median division (see Text-figs. 31 and 32).

A single, w-shaped pelvic scute. No abdominal scutes. Dorsal equidistant between snout and caudal base or a little nearer snout. Pelvic origin below mid-dorsal or below second half of dorsal.

Two species of *Spratelloides* recognized here, each with a subspecies.

- a. A bright and prominent silver mid-lateral band; total anal rays 11-14; scales in lateral series 41-49 ***S. gracilis***
- b. No silver band, but whole lower flank silver; total anal rays 9-11; scales in lateral series 32-46 ***S. delicatulus***

These two species also differ in body depth, head length, post-orbital distance and pectoral length.

Spratelloides gracilis (Schlegel)

(Text-fig. 18)

Clupea gracilis Schlegel, 1846, *Faun. Japon. Poiss.*, pts. 10-14 : 238, pl. 108, fig. 2 (type locality : southeast coasts of Nagasaki).

Clupea argyrotaeniata Bleeker, 1849, *Journ. Ind. Arch.*, **3** : 72 (type locality : Macassar, south-west Celebes).

Spratelloides argyrotaenia Bleeker, 1851, *Natuurk. Tijdschr. Ned. Ind.*, **2** : 214; *Idem*, 1852, *Verh. Bat. Gen., Batavia*, **24** : 29; *Idem*, 1852, *Natuurk. Tijdschr. Ned. Ind.*, **3** : 775; Schultz and Wellander, 1953, *Bull. U.S. nat. Mus.*, **1** (202) : 23-24 (*S. argyrotaeniata*).

Spratelloides gracilis Bleeker, 1853, *Verh. Bat. Gen., Batavia*, **25** : 18; *Idem*, 1892, **6** : 96, pl. (8) 266, fig. 2; Günther, 1868, *Cat. Fishes Brit. Mus.*, **6** : 465 (type of *Clupea argyrotaenia*); Klunzinger, 1871, *Verh. zool.-bot. Ges. Wien*, **21** : 601; Weber and Beaufort, 1913, *Fishes Indo-Aust. Arch.*, **2** : 20, fig. 12; Hardenburg, 1933, *Treubia*, **14** (2) : 215; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 15-16.

- Stolephorus japonicus* (non Lacépède) Jordan and Seale, 1905, *Proc. U.S. nat. Mus.*, **28** : 770; Jordan and Herre, 1906, *Proc. U.S. nat. Mus.*, **31** : 629; Fowler, 1928, *Mem. Bernice P. Bishop Mus.*, **10** : 30; Herre, 1936, *Field Mus. nat. Hist. Zool.*, **21** : 33; Fowler, 1941, *Bull. U.S. nat. Mus.*, **13** (100) : 567 (full synonymy); *Idem*, 1956, *Fishes of the Red Sea and Southern Arabia, Jerusalem*, p. 61, fig. 23.
- Stolephorus gracilis* Evermann and Seale, 1907, *Bull. Bur. Fisher.*, **26** : 53; Whitley, 1953, *Aust. Zool.*, **11** : 332.
- Spratelloides japonicus* Mori, 1928, *Journ. Pan Pacific Res. Inst.*, **3** : 3; Tanaka, 1933, *Jap. Fish. Life Colours*, No. 47; Marshall, 1952, *Bull. Brit. Mus. nat. Hist. (Zool.)*, **1** : 22; Schultz and Wellander, 1953, *Bull. U.S. nat. Mus.*, No. 202 : 24; Morrow, 1954, *Ann. Mag. nat. Hist.*, (12) **7**: 804; Okada, 1955, *Fishes of Japan, Tokyo*: 41; Monroe, 1955, *Marine and freshwater fish. Ceylon* : 28; Jones, 1961, *J. Mar. Biol. Assn. India*, **2** (2), 267-8.
- Spratelloides atrofasciatus* Schultz, 1943, *Bull. U.S. nat. Mus.*, No. 180 : 8, fig. 1; Schultz and Wellander, 1953, *op. cit.* No. 202 : 27, fig. 7.

Note on Synonymy

Only the most important references prior to 1940 are cited here; full synonymies are given by Fowler (1941) under *Stolephorus japonicus*.

The synonymy reveals two main issues. The first is whether the Japanese and other far eastern populations should be separated from those of the Red Sea, Indian Ocean and Indo-Malayan Archipelago. Marshall (1952) showed that his (admittedly few) specimens of *S. gracilis* from the Red Sea had lower pectoral and anal counts than did specimens from Japan (the type locality of Schlegel's *Clupea gracilis*). Schultz & Wellander (1953) were however more emphatic, stating that *gracilis*, as understood by Bertin (1943) and Weber & de Beaufort (1913), actually represented "at least two species"—the "*japonicus*" of Houttuyn, and Bleekers "*argyrotaenia*"—and their finray, scale and gillraker counts seemed to support their conclusion. Counts made on specimens in the British Museum, and supplemented by those of Schultz & Wellander (*loc. cit.*) are given in Text-figs. 15-17. Certainly the counts are higher in the Japanese specimens, but not only do the counts from the extreme boundaries of the geographical range overlap (i.e. Red Sea and Japan), but the specimens of intermediate provenance (i.e. from the Indo-Malayan Archipelago) show intermediate values.

The situation is similar to that found in the Museum specimens of *Dussumieria* (see p. 312) and the same conclusion must be drawn. The populations of *S. gracilis* from any one region cannot be distinguished sufficiently clearly to merit specific distinction. The fact that in numbers of dorsal, pectoral and anal rays and in gillrakers there appears to be the same gradual shift to higher numbers as one proceeds eastwards suggests that this is merely a phenotypic response to some environmental factor, possibly temperature (but cf. *Dussumieria*, p. 316).

A second eastern population which has been separated from *S. gracilis* is *S. atrofasciatus* Schultz, 1943, described from Samoa and distinguished from *S. gracilis* by its lower gillraker and scale counts (Schultz, & Wellander, 1953). In numbers of dorsal, anal and pectoral rays it overlaps *S. gracilis*, but in gillrakers it is rather lower (19-23 on the lower part of the first arch; cf. 26 given as the lowest for *S. argyrotaeniata* by Schultz & Wellander (*loc. cit.*)). This, and its geographical isolation from other populations, suggests that separation from *S. gracilis* would be

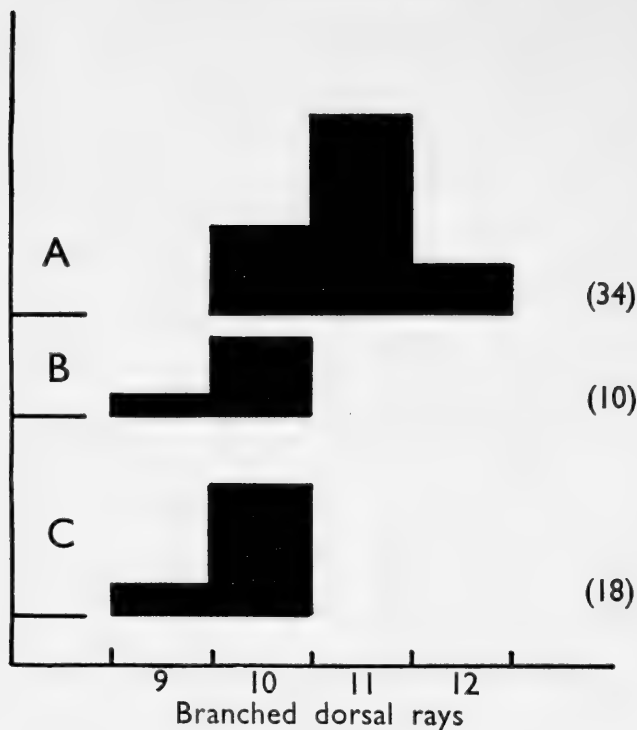


FIG. 15.

Spratelloides gracilis, branched dorsal rays. Dorsal finray frequencies in populations from:

- A. Japan and Formosa.
- B. Indo-Malayan archipelago and Philippines.
- C. Red Sea.

Based on specimens in the British Museum and supplemented by figures from Schultz and Wellander (1953). Numbers in sample placed in parentheses.

justified. But since only a single character is involved (i.e. gillrakers), and since in this character as well as in other meristic counts *S. atrofasciatus* consistently lies at the lower end of the range for *S. gracilis*, there seems good reason to suppose that it represents another ecophenotypic variation of *S. gracilis*. Therefore, I do not believe the Samoan population differs specifically from *S. gracilis*, and I have here given *S. atrofasciatus* subspecific status only in order to emphasize its place amongst the forms included in *S. gracilis*.

The second issue raised by the synonymy is the question of the use of *Stolephorus* Lacépède for a genus of round herring, and the citing of *Atherina japonica* Houttuyn as the genotype of *Stolephorus*.

Some confusion has occurred over the application of the specific name "*japonica*" Houttuyn to a species of *Spratelloides*. Houttuyn (1782) gave a poor description of a Japanese fish, *Atherina japonica*, and Lacépède (1803) placed this fish, together

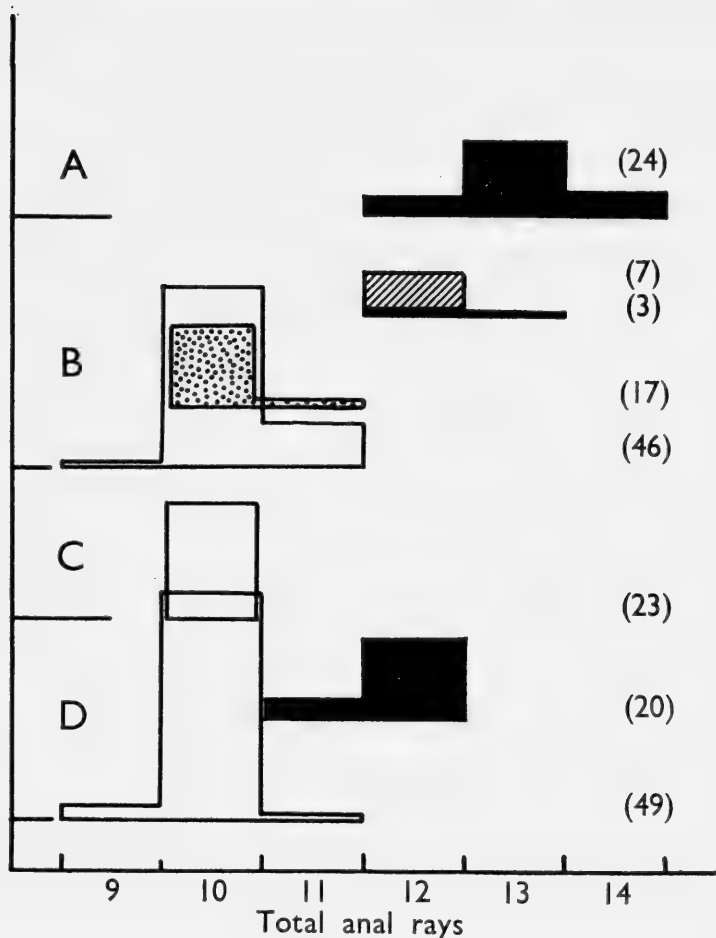


FIG. 16.

Anal finray frequencies in populations of *Spratelloides* from :

- A. Japan and Formosa.
- B. Indo-Malayan archipelago, Philippines and Australia.
- C. Seychelles and Maldives.
- D. Red Sea and Gulf of Aden.

Black *S. gracilis*, White *S. delicatulus*, Hatched *S. argyrotaenia*, Stippled *S. g. robustus* (Australia).

Based on specimens in the British Museum and supplemented by figures from Schultz & Wellander (1953). Numbers in each sample placed in parentheses. N.B.—Both branched and simple rays included in counts.

with an anchovy described but not named by Commerson, in his genus *Stolephorus*. The generic description and figure were evidently based on the latter species, *S. commersonii*, and Opinion 93 given by the International Commission for Zoological Nomenclature directed that *S. commersonianus* (i.e. *S. commersonii*—see footnote,

p. 309) should be the designated genotype of *Stolephorus* and not *Atherina japonica* (Jordan & Gilbert (1883, p. 272) had unfortunately designated the latter previously). The confusion is aggravated because some authors have ignored Opinion 93 and continue to call the round herring genus *Stolephorus* rather than *Spratelloides* (e.g. Fowler, 1941 and 1958, Smith, 1955). At the same time the European anchovy

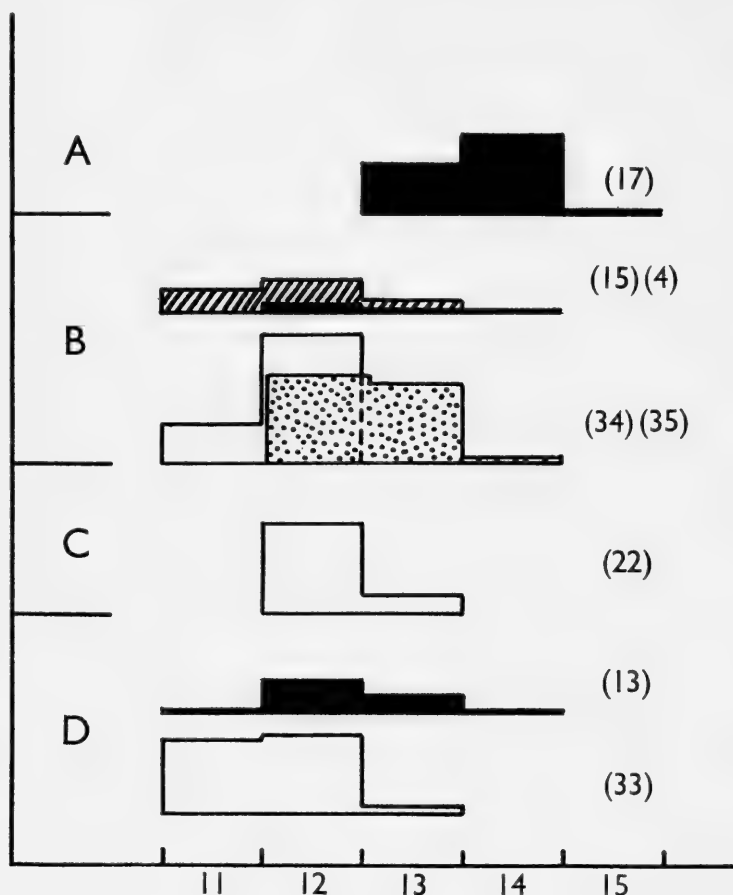


FIG. 17.

Pectoral finray frequencies in populations of *Spratelloides* from :

- A. Japan and Formosa.
- B. Indo-Malayan archipelago and Philippines.
- C. The Seychelles and Maldives.
- D. Red Sea.

Black *S. gracilis*, White *S. delicatulus*, Hatched *S. argyrotaenia*, Stippled *S. robustus* (Australia).

Based on specimens in the British Museum and supplemented by figures from Schultz & Wellander (1953). Numbers in each sample placed in parentheses. The first, unbranched ray included in the counts.

(*Engraulis encrasicholus*) has sometimes been placed in *Stolephorus* (Poll, 1947); its very close Japanese relative is the *Engraulis japonicus* of Schlegel. Thus in Fowler (*loc. cit.*) *Atherina japonica* Houttuyn is cited as the type both of a dussumieriid and an engraulid species. *Stolephorus* should in fact refer only to those Indo-Pacific engraulids which have at least some abdominal scutes (cf. the *encrasicholus* forms which do not, and which should be placed in *Engraulis* Cuvier), normal pectoral rays (cf. the species referred to *Setipinna*), and a maxilla not extending beyond the gill opening (cf. *Thrissocles*). *Stolephorus* is generally a synonym for those Indo-Pacific anchovies otherwise placed in *Anchoviella* Fowler.

If Houttuyn's fish is assumed not to be an *Engraulis*, then *E. japonicus* Schlegel is perfectly correct for the Japanese *encrasicholus*-type anchovy. This assumption is based on the supposition that Houttuyn was familiar with the European *E. encrasicholus* and could have located the similar Japanese form in the *Systema Naturae* (to which he refers in his description). Also, of the three possible Japanese fishes with broad silvery lateral stripes (a character stressed by Houttuyn) only the round herring has 8 pelvic rays, the scuted anchovy and non-scuted (*encrasicholus*-type) anchovy each having only seven. Again, placing his fish in Linnaeus' *Atherina*, Houttuyn may have counted (but not recorded) six branchiostegal rays, which also accords with a spratelloidine. In addition, Houttuyn described a fish with 14 pectoral rays. In 24 specimens of *Spratelloides* from Japan, I counted 14 rays in 5 fishes, 13 rays in 15 fishes, and 12 rays in 4 fishes (see Text-fig. 17). Five specimens of *Engraulis* from Japan had 16–18 rays, but in seven specimens of *Stolephorus* from China there were 13 rays. The rays are however, extremely difficult to count in the smaller dussumieriids and perhaps too much reliance should not be placed on Houttuyn's count.

The remaining details of Houttuyn's description could fit all three Japanese fishes (mouth toothless, head scaleless), but the dorsal count of 5 is surely a mistake. He mentions size—4 inches—but says "*Ook heb ik 'er een van drie Duimen*" (which suggests that Jordan & Evermann (1917) were perhaps wrong in thinking that the fish was described from rough notes or memory).

To resolve the matter, two courses are open. Either *japonica* Houttuyn 1782 is considered a *nomen dubium*, there being no type specimen nor adequate description; or one of the three Japanese species with a broad silvery lateral stripe is accepted as Houttuyn's fish. I favour the first course, for although Houttuyn's description probably fits a dussumieriid fish of the genus *Spratelloides* better than it does an anchovy, there is no further evidence that can be produced which will confirm the identity of this fish. *Spratelloides japonica* Houttuyn should therefore be suppressed in favour of *S. gracilis* (Schlegel) as the first recognizable description of this species. Application has been made to the International Commission for Zoological Nomenclature to this effect.

DESCRIPTION. Based on nineteen fishes, 59.0–93.0 mm. standard length, including the lectotype (a specimen 66.7 mm. S.L. believed by Günther (1868) to be Bleeker's type from the East Indian Archipelago), and from Japan (15) and Formosa (3). In addition, all other specimens listed under Study Material (p. 375) used for meristic counts.



FIG. 18.

Spratelloides gracilis. From a specimen 90 mm. standard length, Wakanoura, Japan.
Scales omitted.

In percentages of standard length : body depth (under dorsal origin) 13.2–17.3, head length¹ 22.0–24.5, snout length 6.9–8.2 ; eye diameter 5.3–6.3, post-orbital distance² 7.4–8.5, maxilla length 8.1–9.0, pectoral length 11.6–12.2, pelvic length 9.4–9.8, pre-dorsal distance 47.0–50.0 (one fish 52.3), pre-pelvic distance 53.5–58.7, pre-anal distance 79.0–84.7.

Body slightly compressed, its depth less than head length. Snout pointed, a little larger than eye diameter. Maxilla longer than snout, passing front border of eye but not reaching pupil. Post-orbital a little larger than snout length. Dorsal origin equidistant, or usually just nearer snout than caudal base. Pelvic origin under middle or second half of dorsal, a little nearer to caudal base than to snout.

Dorsal ii 9–12 (see Text-fig. 15), pectoral i 10–15 (see Text-fig. 17), pelvic i 7, anal 11–14, of which ii or iii are branched (see Text-fig. 16).

Gillrakers 20–37 on the lower part of the first arch (including one at angle) and 7–12 above angle.

Scales in lateral series 41–49 (based partly on Schultz & Wellander (*loc. cit.*) and Bertin, 1943) ; 8–9 transverse rows.

Vertebrae 46 (3 specimens, Bertin (*loc. cit.*)).

TYPE. East Indian Archipelago. Lectotype, B.M. (N.H.), 1867.11.28.17.

COLOUR IN ALCOHOL. Upper and lower surfaces brown, divided by a broad lateral silver stripe, whose greatest width just exceeds eye diameter ; in some specimens the lateral band is dark brown or black, much darker along its upper margin ; and in all Japanese specimens examined the silvery stripe is outlined above by a thin, dark brown line. In some specimens a dark brown or black line dorsally from nape to caudal. Glandular scales on caudal not, or but faintly pigmented (cf. *S. delicatulus*).

DISTRIBUTION. Indo-Pacific region, from Red Sea to Japan ; southwards along African coast to Pemba (Morrow, 1954) ; in Pacific, southwards to Samoa ; Indian Ocean, Ceylon and Laccadive Sea (Jones, 1961).

¹ The longest measurement, i.e. premaxillary symphysis to posterior border of operculum *below* the indentation in the latter characteristic of *Spratelloides*. The measurement is thus not along a horizontal line.

² The shortest distance, i.e. from posterior eye border to centre of indentation in operculum.

Two subspecies recognized here.

- a. Gillrakers on lower part of first arch 24-37; scales in lateral series 44-49; total anal rays 11-14; Indo-Pacific region excluding Samoa . *Spratelloides gracilis gracilis*
- b. Gillrakers on lower part of first arch 19-23; scales in lateral series 41-42; total anal rays 10-11; restricted to Samoa . . . *Spratelloides gracilis atrofasciatus*

Spratelloides gracilis gracilis Schlegel

Spratelloides gracilis Schlegel, 1846, *Faun. Japon. Poiss.*, pts. 10-14; 238, pl. 108, fig. 2 (for full synonymy, see under species).

DESCRIPTION AND DIAGNOSIS. Distinguished from the Samoan subspecies by a higher gillraker count (24-37) and more scales in lateral series (44-49). Dorsal ii 9-12, pectoral i 10-14, pelvic i 7, anal 11-14 (including ii or usually iii simple rays).

DISTRIBUTION. As for species, but not found in Samoa.

TYPE. *S. gracilis* Schlegel.

Spratelloides gracilis atrofasciatus Schultz

Spratelloides atrofasciatus Schultz, 1943, *Bull. U.S. nat. Mus.*, No. 180: 8, fig. 1; *Idem*, 1953, *op. cit.*, No. 202: 24.

DESCRIPTION AND DIAGNOSIS. A Samoan population distinguished from *S. g. gracilis* by its lower gillraker count (19-23) and fewer scales in lateral series (41-42). Dorsal ii 9-10, pectoral i 10-11, pelvic i 7, anal 10-11 (including ii or usually iii simple rays). Description based on Schultz.

DISTRIBUTION. Samoa only.

TYPE. *S. atrofasciatus* Schultz.

Spratelloides delicatulus (Bennett)

(Text-fig. 19)

Clupea delicatula Bennett, 1831, *Proc. zool. Soc. London*, 1: 168 (Type locality: Mauritius).

Clupea macassariensis, Bleeker, 1849, *Journ Indian Arch.*, 3: 72.

Clupeoides macassariensis Bleeker, 1851, *Natuurk. Tijdschr. Ned. Ind.*, 2: 214; *Idem*, 1852, *Verh.*

Bat. Gen., Batavia, 24: 17; *Idem*, 1852, *Natuurk. Tijdschr. Ned. Ind.*, 3: 772.

Alosa alburnus, Kner, 1867, *Sitzb. K. Akad. Wiss. Wien*, 54: 387, pl. 1, fig. 16.

Spratelloides alburnus Günther, 1868, *Cat. Fishes Brit. Mus.*, 7: 464.

Stolephorus alburnus Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100: 565.

Spratelloides delicatulus Günther, 1868, *Cat. Fishes Brit. Mus.*, 7: 464; Bleeker, 1872, *Atlas.*

Ichth. Ind. Néerland., 6: 96, pl. 264, fig. 3; Günther, 1910, *J. Mus. Goddefroy, Hamburg*, 6:

383; Weber and Beaufort, 1913, *Fishes Indo-Aust. Arch.*, 2: 20; Gilchrist and Thompson,

1917, *Ann. Durban Mus.*, 1: 296; Barnard, 1925, *Ann. S. Afr. Mus.*, 21 (1): 110; Harden-

berg, 1933, *Treubia*, 14 (2): 216; Roxas, 1934, *Philipp. J. Sci.*, 55: 249; Bertin, 1943, *Bull.*

Inst. océanogr. Monaco, No. 853: 18; Marshall, 1950, *Bull. Raffles Mus.*, No. 22: 168; *Idem*,

1952, *Bull. Brit. Mus. nat. Hist. (Zool.)*, 1: 222; Schultz and Wellander, 1953, *Bull. U.S.*

nat. Mus., No. 202: 26; Morrow, 1954, *Ann. Mag. nat. Hist.*, (12) 7: 804; Randall, 1955,

Atoll Res. Bull., No. 47: 6; Fowler and Steinitz, 1956, *Bull. Res. Council Israel*, 5, 13 (3-4):

262; Rofen, 1958, *Nat. Hist. Rennell Is., Brit. Solomon Is.*, 1, *Copenhagen*: 151; Jones,

1960, *J. Mar. biol. Ass. India*, 2 (1): 103; *Idem*, 1961, *op. cit.*, 2 (2): 267.

Stolephorus delicatulus Jordan and Seale, 1906, *Bull. Bur. Fisher.*, **25** : 186 ; Evermann and Seale, 1906, *Bull. Bur. Fisher.*, **26** : 53 ; Fowler, 1928, *Mem. Bernice P. Bishop. Mus.*, **10** : 29 ; Whitley, 1929, *Proc. Linn. Soc. N.S.W.*, **54** : 92 ; Herre, 1936, *Field Mus. nat. Hist. Zool.*, **21** : 32 ; Fowler, 1941, *Bull. U.S. nat. Mus.*, No. 100 : 562 ; Smith, 1955, *Ann. Mag. nat. Hist.*, (12) **8** : 307.

Spratelloides robustus Ogilby, 1897, *Proc. Linn. Soc. N.S.W.*, **22** : 64 (Type locality : coast of New South Wales) ; Bertin, 1943, *Bull. Inst. océanogr. Monaco*, No. 853 : 16.

Stolephorus robustus Waite, 1904, *Mem. New South Wales Nat. Club*, No. 2 : 12 ; McCulloch, 1920, *Rec. Austral. Mus.*, **13** (2) : 42, pl. 11, fig. 1 ; McCulloch and Whitley, 1925, *Mem. Queensland Mus.*, 8 (2) : 131 ; McCulloch, 1927, *Fishes of New South Wales*, ed. 2 : 16, pl. 4, fig. 51a ; Blackburn, 1941, *Bull. Counc. sci. ind. Res. Aust.*, No. 138 : 59.

A fuller synonymy is given by Fowler (1941) under *Stolephorus delicatulus*, *S. robustus* and *S. alburnus*.

Notes on Synonymy

The problem of *Stolephorus* has already been discussed. *Spratelloides alburnus* (Kner), erroneously described from "Valparaiso, Chile"—in fact from Samoa—is almost certainly *S. delicatulus*, which has been recorded from the Marshall Is. and may well occur to the south (Schultz & Wellander, 1953). Bertin (1943) reached the same conclusion.

The only major change from previous synonymies is the inclusion of *S. robustus*. In proportional measurements and in all meristic counts except scales, the specimens of *S. robustus* in the Museum (all from New South Wales) fall within the ranges of *S. delicatulus* (see Table III), and I have been unable to find any colour differences. Unfortunately insufficient specimens of either species have had a full series of scales, and the descriptions of Fowler (1941), Bertin (1943) and Schultz & Wellander (1953) vary somewhat (respectively 32–36, 35–38, 40–42 in lateral series for *S. robustus*, and 36–40, 43–45, 45–46 for *S. delicatulus*). All are agreed however that the New South Wales population has the lower count, and on this basis I believe that it should be considered a subspecies of *S. delicatulus*. There is also a tendency for the New South Wales population to have a slightly longer pelvic fin (Table III) and slightly more rays in the pectoral (Text-fig. 17) but the differences are small.



FIG. 19.

Spratelloides delicatulus. From a specimen 69 mm. standard length, Hasler Collection (locality not stated). Scales omitted.

DESCRIPTION. Based on thirteen fishes (*S. delicatulus*), 39.0–52.0 mm. standard length from the Maldives, Thousand Is., Bonham Is., and the Seychelles; and ten fishes (*S. robustus*) 50.3–71.0 mm. standard length from the coast of New South Wales. Additional meristic counts made on other specimens listed under Study Material (p. 376). Single measurements outside normal range are placed in parenthesis.

In percentages of standard length: body depth (16.7) 17.9–21.0, head length¹ 24.0–28.2, snout length 6.6–7.7, eye diameter 6.5–7.7, post-orbital distance 8.8–10.3, maxilla length 8.4–9.6, pectoral length (11.9) 14.0–15.8, pelvic length 9.2–12.8, pre-dorsal distance 45.6–49.2, pre-pelvic distance (50.5) 53.0–57.5, pre-anal distance (75.0) 76.2–83.5.

Body slightly compressed, rounder than in *S. gracilis*, its depth less than head length. Snout pointed, a little larger than eye diameter. Maxilla longer than snout, reaching almost to pupil of eye. Post-orbital a little longer than snout. Dorsal origin equidistant, or usually nearer snout than caudal base. Pelvic origin under mid-dorsal or under second half of dorsal, a little nearer to caudal base than to snout.

Dorsal ii 9–11, pectoral i 10–13 (see Text-fig. 17), pelvic i 7, anal 9–11 of which ii or iii are branched (see Text-fig. 16).

Gillrakers 26–33 on the lower part of the first arch (including one at angle), 9–11 on upper part.

Scales in lateral series 32–46, 7–9 transverse.

Vertebrae 42–44 (Bertin, 1943).

TYPE. Mauritius.

COLOUR IN ALCOHOL. Upper surfaces grey-blue or brown, sides and ventral surfaces white or silvery, the two areas meeting at an abrupt line dorso-laterally. Top of head, tip of snout, lower jaw and tongue dark brown and a small black spot in front of eye. Two black streaks along glandular scales on each lobe of caudal.

DISTRIBUTION. Eastern coast of Africa, from Natal, northwards to Gulf of Aden and Red Sea; India, East Indies, Philippines, Cocos-Keeling Is., Hawaii; New South Wales, Queensland, Tasmania. *S. delicatulus* apparently does not penetrate as far north as *S. gracilis*, but reaches further south (i.e. to Australia).

Two subspecies recognized here.

- a. Scales in lateral series 36–46; pelvic fins 9.2–11.5 % of standard length; pectoral finrays i 10–12; Indo-Pacific region excluding Australia

Spratelloides delicatulus delicatulus

- b. Scales in lateral series 32–42; pelvic fins 11.1–12.8 % of standard length; pectoral finrays i 11–13; confined to Australian coasts

Spratelloides delicatulus robustus

Spratelloides delicatulus delicatulus Bennett

Spratelloides delicatulus Bennett, 1831, *Proc. Comm. zool. Soc. London*, 1: 168 (for full synonymy, see species).

¹ Measurements as in *S. gracilis*, footnote, p. 344.

DESCRIPTION AND DIAGNOSIS. Distinguished from the Australian subspecies by its greater number of scales in lateral series, although authors are not agreed on the precise range in this character (see p. 346). It also has slightly shorter pelvic fins (9.2–11.5% of standard length) and fewer pectoral rays (i 10–12).

DISTRIBUTION. As for species but excluding the coasts of Australia.

TYPE. *Spratelloides delicatulus* (Bennett.)

Spratelloides delicatulus robustus Ogilby

Spratelloides robustus Ogilby, 1897, *Proc. Linn. Soc. N.S.W.*, **22** : 64 (see under species for full synonymy).

DESCRIPTION AND DIAGNOSIS. An Australian population differing from *S. d. delicatulus* in having fewer scales in lateral series (32–42), slightly longer pelvic fins (11.1–12.8% of standard length), and slightly more rays in the pectoral (i 11–13).

DISTRIBUTION. Queensland, New South Wales, Victoria, Tasmania (after Fowler, 1941).

TYPE. Coast of New South Wales, Australia. Australian Museum, Sydney, No. 1. 3668.

JENKINSIA Jordan & Everman

Jenkinsia Jordan and Evermann, 1896, *Bull. U.S. nat. Mus.*, **50** : 418 (genotype *Dussumieria stolifera* Jordan and Gilbert).

DESCRIPTION. Body elongate, slightly compressed, rounded ventrally; snout pointed, jaws equal or lower slightly projecting. A single (posterior) supra-maxilla, paddle-shaped with a slender anterior shaft; maxilla toothed. Premaxilla with or without a single series of fine conical teeth. Little or no development of fleshy eminence (cleithral flap) at postero-ventral angle of gill-opening. Posterior border of operculum strongly indented, more so than in *Ehirava*. Sub-operculum rectangular, posterior border not rounded but forming a well-defined and slightly obtuse angle. Inter-operculum exposed and three or four branchiostegal rays visible externally. Posterior border of pre-operculum vertical.

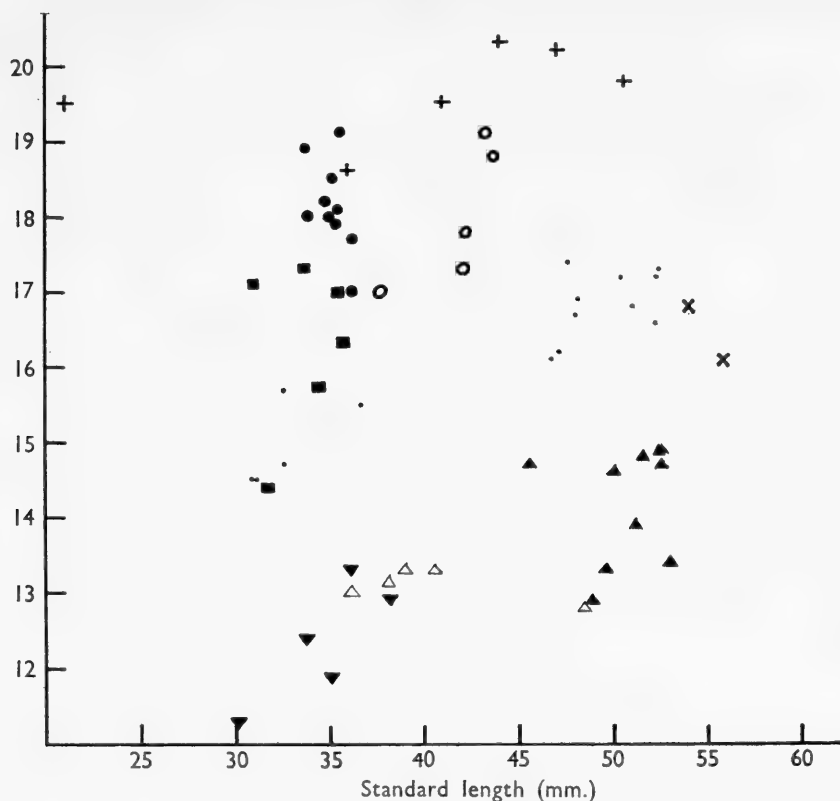
A pair of posterior fontanelles becoming reduced in size in adults. Anterior frontal fontanelle present in smaller fishes, sometimes in adults.

A single w-shaped pelvic scute. No abdominal scutes. Dorsal a little nearer snout than caudal base. Pelvic origin below mid-dorsal.

A bright silvery midlateral stripe along flanks.

The Species of Jenkinsia

Authors have recognized variations in finray and gillraker counts amongst specimens of *Jenkinsia* from different parts of the Caribbean region, and several species have been based on these. But Parr (1930), Beebe & Tee-Van (1933) and Longley & Hildebrand (1941) all believed that the overlap between finray counts in such populations was too great for any one population to be separated at specific level.



Body depth expressed as percentage of standard length (ordinate) plotted against standard length (abscissa) in various populations of *Jenkinsia*.

J. lamprotaenia

- × Jamaica (types of *J. lamprotaenia*).
- Cat Cay, Bahamas.
- Key West (types of *Dussumieria stolistera*).
- St. John, Virgin Islands.
- + Venezuela (figures from Martin, 1955).

J. majua

- ▲ Campeche Banks.
△ Swan Island.
▼ Gun Cay, Bahamas.

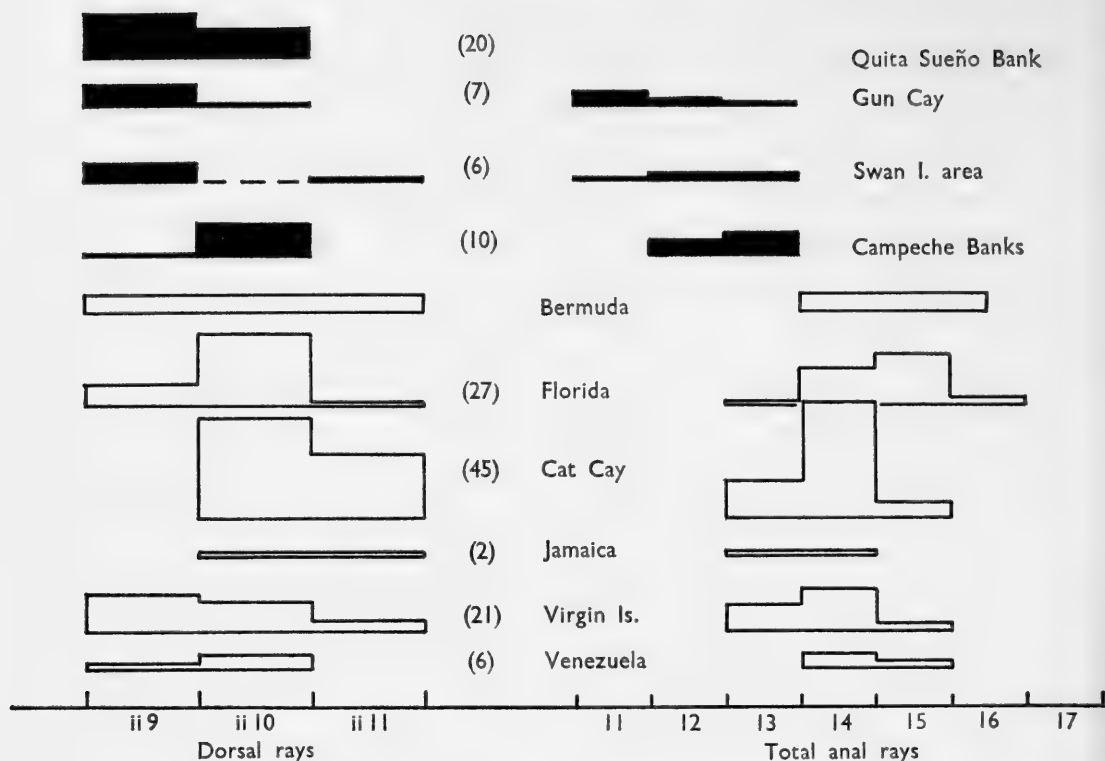


FIG. 21.

Dorsal and anal finray count frequencies in populations of *Jenkinsia*.

Black, *J. majua*; White, *J. lamprotaenia*.

Numbers in sample placed in parentheses. Range only for Bermuda specimens (based on published records—see text).

the part of the head immediately behind the junction of the two inner arms of the transverse frontal sensory canal is domed or flat (again, especially in juveniles) (Text-fig. 32b). In the other group however, the posterior fontanelles are divided anteriorly by a broad wedge, and within this wedge is a triangular depression in which lies a median branch of the post-frontal canal (Text-fig. 32a).

There is also a difference in the size of the fish at which the frontals start to extend posteriorly to close the fontanelles. In the first group this occurs at a larger size than in the second, and in this the former resemble *Spratelloides*, while the second group resemble rather the genera of the Ehiravini.

These two differences are important because they also help to separate the Ehiravini from *Spratelloides*. But for the geographical isolation of *Jenkinsia*, a direct evolution of the Ehiravini from those members of *Jenkinsia* which have premaxillary teeth and a wedge of bone separating the posterior fontanelles would

seem clear. As it is, *Jenkinsia* may have become isolated at a time when *Spratelloides* had only just begun to diverge (through loss of premaxillary teeth, development of the cleithral flap and retention of the second supra-maxilla).

A third character which can be correlated with the tooth and fontanelle characters is the higher number of rays in the anal fin in those fishes with a toothed premaxillary. In addition these fishes also tend to be deeper bodied (Text-fig. 20) although body depth shows positive allometry with standard length and the difference is difficult to define when all size groups are considered.

A final difference between populations of *Jenkinsia* involves gillraker numbers. This is here interpreted as a subspecific character.

- a. Premaxilla toothed ; posterior fontanelles divided anteriorly by wedge of bone, with triangular depression in front ; anal rays 13-16 ; body deeper, its depth usually over 15% of standard length *J. lamprotaenia*
- b. Premaxilla edentulous ; posterior fontanelles narrowly divided anteriorly, area in front domed, becoming flat in adults ; anal rays 11-13 ; body more slender, its depth usually under 15% of standard length *J. majua* sp. nov.

The geographical distribution of these two species overlaps in the Bahamas (where I have examined specimens of the first from Cat Cay, and of the second from the nearby Gun Cay) and in the Gulf of Campeche. Further distributional records are required, but on the basis of the present specimens, *J. lamprotaenia* seems to occur mainly along the outer boundary of the area (i.e. Bermuda, the islands of the West Indies and Antilles, Venezuela), while *J. majua* appears to be a more western species (Gulf of Campeche, Swan Island, British Honduras).

Jenkinsia lamprotaenia (Gosse)

(Text-fig. 23)

Clupea lamprotaenia Gosse, 1851, *Naturalist's Sojourn in Jamaica* : 291, pl. 1, fig. 2 (Type locality : Jamaica).

(*Spratelloides*) *lamprotaenia* Günther, 1868, *Cat. Fish Brit. Mus.*, 7 : 465.

Dussumieria stolidifera Jordan and Gilbert, 1884, *Proc. U.S. nat. Mus.*, 7 : 25 (Type locality : Key West, Florida).

Jenkinsia stolidifera Jordan and Evermann, 1896, *Bull. U.S. nat. Mus.*, No. 47 (pt. 1) : 418 ; Fowler, 1930, *Proc. biol. Soc. Wash.*, 43 : 145.

Jenkinsia lamprotaenia Jordan and Evermann, 1896, *Bull. U.S. nat. Mus.*, No. 47 : 419 ; Parr, 1930, *Bull. Bingham oceanogr. Coll.*, 3 (4) : 3 ; Beebe and Tee-Van, 1928, *Zoologica*, 10 (1) : 43 ; *Idem*, 1933, *Zoologica*, 13 (7) : 136 ; Longley and Hildebrand, 1941, *Pap. Dep. mar. Biol. Carnegie*, 34 (No. 535) : 12 ; Fowler, 1944, *Monagr. Acad. nat. Sci. Philad.*, No. 6 : 123 ; Martin, 1955, *Mem. Soc. Cienc. nat. La Salle*, 15 : 185.

Stolephorus viridis Bean, 1912, *Proc. biol. Soc. Wash.*, 25 : 122 (Type locality : Bermuda).

Jenkinsia bermudana Rivas, 1946, *Smithson. Misc. Coll.*, 106 (14) : 2, fig. 1, pl. 1 (Type locality : Bermuda).

Jenkinsia viridis Collette, 1962, *Copeia*, No. 3 : 659.

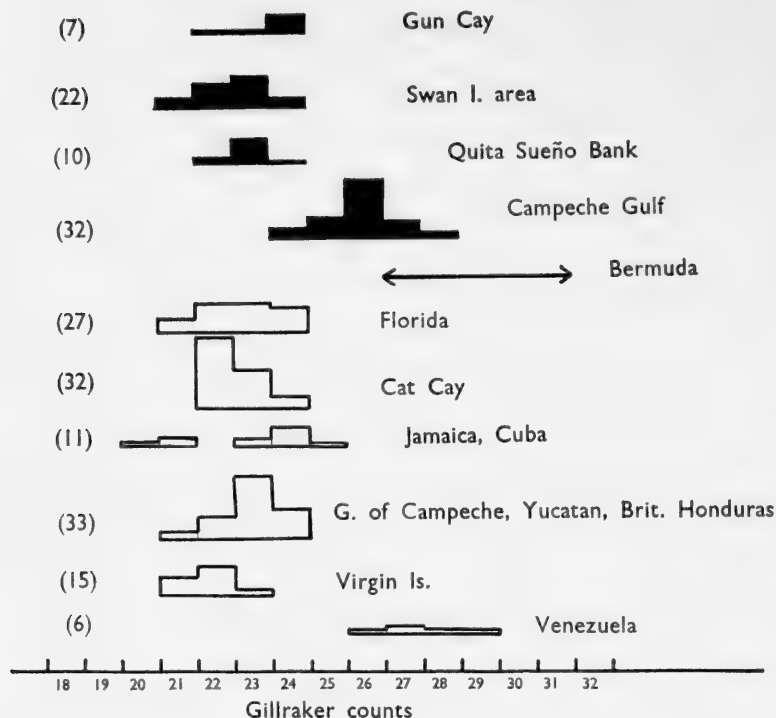


FIG. 22.

Gillraker count frequencies in populations of *Jenkinsia*.

Black, *J. majua*; White, *J. lamprotaenia*.

Numbers in sample placed in parentheses. Rakers counted on lower part of first arch, including one at angle when present.

Note on Synonymy

As already outlined under the generic notes, two principal non-meristic characters are here used to define the species. I have examined the types of *Clupea lamprotaenia* and *Dussumieria stolifera*, and in both cases premaxillary teeth are present, and the posterior fontanelles are divided anteriorly by a wedge of bone, in front of which is a triangular depression. I have also examined specimens from Cat Cay (Bahamas), St. John (Virgin Islands), Monroe County (Florida), the Cayman Islands, Cuba, British Honduras, and the Gulf of Campeche, and these agree with the types. Recently Collette (1962) has re-examined Bean's four type specimens of *Stolephorus viridis* and has shown that in fact two species are represented. The first species, which has a gillraker count of 37 and 39, he believes to be the only Bermuda species; the second, represented by two rather damaged specimens with gillraker counts of 30 and 32, he places with *J. lamprotaenia* and, since there is no other evidence of this species in Bermuda, believes the specimens to have been included in error. He places *J. bermudana* Rivas in the synonymy of *J. viridis*, and informs me (*in litt.*) that the types of both these two species have premaxillary

teeth. Since the presence of premaxillary teeth is so exactly correlated with the fontanelle character there seems little reason to separate the Bermuda species from *J. lamprotaenia* at specific level; I agree however that the specimens with low gill-raker counts from Bermuda may well have come from another locality.

The pre-maxillary teeth are usually obvious and I have seen them in the smallest specimen available, a fish of only 18 mm. Although the teeth may be deciduous, the complete series rarely occurring, some can always be found.

On the basis of published descriptions, the fishes from Bermuda and from Venezuela can clearly be distinguished on gillraker counts (see Text-fig. 22), both having similar and much higher counts than the rest. In numbers of dorsal and anal rays however, there is no evidence (Text-fig. 21) that any one population of *J. lamprotaenia* differs significantly from the rest, although no fishes with only 11 dorsal rays have been recorded from Jamaica or Cat Cay. The latter two populations also agree in being more slender (Text-fig. 20—small dots and crosses) but more specimens are required before they can be positively separated from the Florida and other populations. In turn, the Florida fishes have slightly larger eyes (9.1–11.5% of standard length in the size group 31–36 mm.; compared with 7.7–8.9 in specimens from Jamaica and Cat Cay of 31–55 mm.), but fishes from the Virgin Islands are intermediate and closely resemble the Jamaica specimens (8.5–9.0% in fishes of 37–43 mm.).

Thus on the basis of the present collections there is reason to believe that only the Bermuda and Venezuela populations have diverged sufficiently to be recognized as a distinct subspecies.

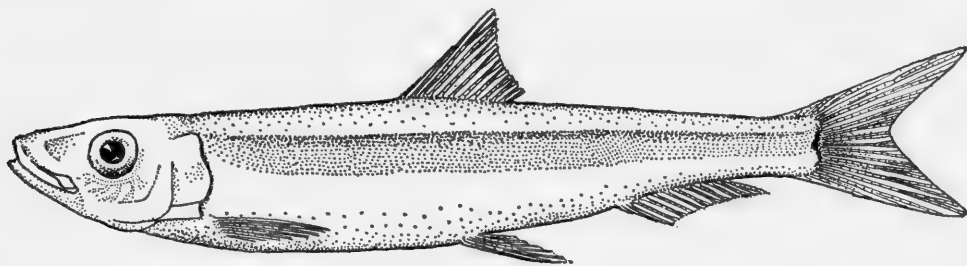


FIG. 23.

Jenkinsia lamprotaenia. From a specimen 51 mm. standard length, Cat Cay, Bahamas. Scales omitted.

DESCRIPTION. Based on the types of *Clupea lamprotaenia* (54.0 and 55.8 mm.) from Jamaica, ten fishes (46.7–52.4 mm.) from Cat Cay (Bahamas), five of the types of *Dussumieria stolidifera* (31.0–35.7 mm.) from Key West (Florida), ten fishes (33.9–36.2 mm.) from Monroe County (Florida), and five fishes (37.7–43.3 mm.) from St. John (Virgin Islands). Meristic counts include 101 specimens (see Text-figs. 20–22).

In percentages of standard length: body depth 14.4–19.1, head length¹ 23.5–28.7, snout length 7.3–9.1, eye diameter 7.7–11.5, post-orbital distance 7.9–9.6, pectoral

¹ Measured to indentation of posterior margin of operculum, i.e. a horizontal measurement; cf. *Spratelloides*, p. 344.

length 12.8-16.8, pelvic length 10.7-13.9, pre-dorsal distance 44.8-50.1, pre-pelvic distance 52.2-58.5, pre-anal distance 71.0-82.0.

Body moderately compressed, its depth much less than head length. Snout pointed, equal to eye (except in Florida and Virgin Islands specimens). Maxilla reaching beyond front border of eye, but not to pupil. Post-orbital equal or larger than snout, larger than eye (except in Florida and Virgin Islands specimens).

Posterior fontanelles broadly separated by wedge of bone (frontals) anteriorly, as shown in Text-fig. 32a. A shallow triangular depression in front of fontanelles containing a branched posterior portion of the transverse frontal sensory canal.

Premaxilla with a single series of conical pointed teeth, often deciduous. Dorsal origin a little nearer snout than caudal base or equidistant. Pelvic origin under middle of dorsal, nearer to caudal base than to snout. Anal origin equidistant between pelvic origin and caudal base.

Dorsal ii 9-11, pectoral i 11-13, pelvic i 7, anal ii-iii 10-13 (total 13-16).

Gillrakers 20-31 on the lower part of the anterior arch (including one at angle).

Scales in lateral series approximately 35-40.

Vertebrae 38 (in a type specimen of *Dussumieria stolifera*).

SYNTYPES. Jamaica. B.M. (N.H.), 1962.7.19.3-4.

COLOUR IN ALCOHOL. Back and sides light brown, with a double line of melanophores down back and extending forwards along frontals to premaxillary symphysis. A broad silvery band along flanks, almost as wide as eye diameter. Lower flanks and belly light brown or cream. Pigment at base of caudal fin.

DISTRIBUTION. Bermuda, Bahamas, Florida; Cuba, Jamaica to Puerto Rico and Virgin Islands; Gulf of Campeche and British Honduras; Venezuela (see Martin, 1955).

Two subspecies are described here, the Bermuda and Venezuela fishes being separated from the rest by their high gillraker count. Although the latter two populations are also well separated geographically from each other (as in the case of the Red Sea and China populations of *Dussumieria*), they both differ so sharply from the remainder that I am forced to recognize them as distinct; future work may well show differences between the two.

Jenkinsia lamprotaenia lamprotaenia (Gosse)

Clupea lamprotaenia Gosse, 1851, *Naturalists Sojourn in Jamaica*: 291, pl. 1, fig. 2 (Type locality: Jamaica). (For remainder of synonymy, see under species for *Dussumieria stolifera* and *Jenkinsia lamprotaenia*).

DIAGNOSIS. Distinguished from Bermuda and Venezuela populations by its lower gillraker count (20-24) as shown in Text-fig. 22.

TYPE. *J. lamprotaenia* (Gosse), Jamaica (syntypes in Brit. Mus. (Nat. Hist.)).

Jenkinsia lamprotaenia viridis (Bean)

Stolephorus viridis Bean, 1912, *Proc. biol. Soc. Wash.*, 25: 122 (Type locality: Bermuda).

Jenkinsia lamprotaenia Hollister, 1936, *Zoologica*, 21 (4): 276, figs. 40-44 (Caudal skeleton).

Jenkinsia bermudana Rivas, 1946, *Smithson. Misc. Coll.*, 106 (14): 2, fig. 1, pl. 1 (Type locality: Bermuda).

DIAGNOSIS. Distinguished from above by its higher gillraker count (26-31) as shown in Text-fig. 23.

TYPE. *Stolephorus viridis* Bean, Bermuda (U.S.N.M. 74084).

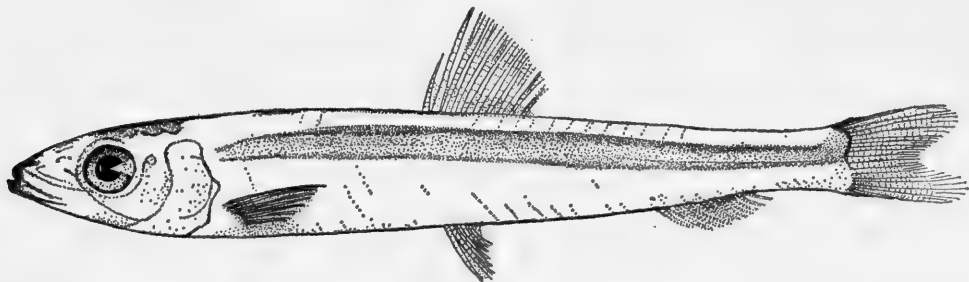


FIG. 24.

Jenkinsia majua sp. nov. Holotype, 53.8 mm. standard length.
(Drawn by Miss Carolyn Reusch.)

***Jenkinsia majua* sp. nov.**

(Text-fig. 24)

DESCRIPTION. Based on the type and seventeen other fishes (45.7-53.8 mm.) from Arcas Cay, Campeche Bank, six fishes (29.3, 36.1-48.4 mm.) from Swan Island, and five fishes (30.1-38.2 mm.) from Gun Cay, Bahamas.

In percentages of standard length: body depth (10.6) 11.3-14.9, head length 20.5-24.4, snout length (6.6) 7.1-8.3, eye diameter 5.3-7.6, post-orbital distance 7.2-9.2, pectoral length 10.3-12.3, pelvic length 8.4-11.8, pre-dorsal distance 45.5-51.0, pre-pelvic distance 49.0-57.5, pre-anal distance 73.0-81.3.

Body moderately compressed, its depth much less than head length. Snout pointed, greater than eye diameter. Maxilla reaching to just beyond anterior eye border, but not to pupil. Post-orbital roughly equal to snout length.

Posterior fontanelles narrowly divided by arm of supra-occipital; a small wedge of bone only between anterior ends of fontanelles (see Text-fig. 32b); frontals domed or flat in front of fontanelles.

Pre-maxillary teeth either absent, or so deciduous that none have been found.

Dorsal origin a little nearer snout than caudal base or just equidistant. Pelvic origin below middle of dorsal, nearer to caudal base than to snout, and nearer anal origin than pectoral base. Anal origin equidistant between pelvic origin and caudal base.

Dorsal ii 9-11, pectoral i 11-12, pelvic i 7, anal ii-iii 9-11 (total 11-13).

Gillrakers 21-28 on lower part of anterior arch (including one at angle when present).

Scales in lateral series approximately 35-40.

COLOUR IN ALCOHOL. Uniform light brown with broad lateral silvery streak a little narrower than eye. Two lines of melanophores down back. Base of caudal pigmented.

DISTRIBUTION. Gulf of Campechè ; Swan Island and Gun Cay (Bahamas) ; and NW. coast of Caribbean Sea.

I would like to record here my gratitude to Dr. Loren P. Woods of the Chicago Natural History Museum for his generosity in allowing me to describe this new species after he had himself begun a preliminary description, and also for so willingly making his material available to me. I have retained the specific name *majua* chosen by him, which is the Cuban name for *Jenkinsia* spp.

Specimens of *J. majua* from Gun Cay and from localities in the Caribbean have a lower gillraker count than do those from the type locality, Campeche Bank (see Text-fig. 22). The difference is one of modal numbers, but the overlap between the two groups is slight, three specimens from Campeche Bank having a low count. The Campeche population seems to be sufficiently isolated from the rest (at least as far as the available material can indicate) for this difference to be given sub-specific rank. No other differences have been found.

- | | | | | | |
|----|--|---|---|---|------------------------|
| a. | Gillrakers on lower part of anterior arch 24-28, mode 26 | . | . | . | <i>J. majua majua</i> |
| b. | Gillrakers on lower part of anterior arch 21-24, mode 23 | . | . | . | <i>J. majua woodsi</i> |

Jenkinsia majua majua

Distinguished by a slightly higher range and modal gillraker count. Apparently confined to the Gulf of Campeche and an area to the north of Yucatan.

TYPE. *J. majua* (see list of Study Material).

Jenkinsia majua woodsi subsp. nov.

Distinguished from the above by a slightly lower range and modal gillraker count. Distributed in the Bahamas (Gun Cay), and the N.W. coast of the Caribbean (British Honduras, Swan I., Quita Sueño and Serrano Cays).

Named for Dr. Loren P. Woods.

HOLOTYPE AND PARATYPES. See list of Study Material.

SYSTEMATIC CHARACTERS

In the following section are discussed certain dussumieriid features which are of value in defining subfamilies, tribes, genera and species. Some, such as scutes, have not been utilized before ; others have either been missed or have received passing mention only.

Scutes

Although the round herrings generally lack scutes, all possess in one form or another a single scute lying immediately in front of the pelvic fin. This scute was figured by Chapman (1948) for *Etrumeus*. It is essentially similar to the w-shaped scute shown here for *Spratelloides delicatulus* (Text-fig. 25) and it is found also in *Dussumieria* and in all members of the tribe Spratelloidini. Chapman (*loc. cit.*) shows a second, triangular scute just between the pelvic fin bases in *Etrumeus* ;

I have not found this in *Dussumieria* nor in the *Spratelloidini*. The anterior scute has been referred to as a "modified" scute (Chapman *loc. cit.*, Whitehead 1962a), but this may imply an erroneous direction to scute evolution (see p. 367 below).

A second type of pelvic scute is found in the *Ehiravini*. This scute more closely resembles the typical clupeid scute, having lateral ascending arms rising just in front of the pelvic fins, but the central portion of the scute is rounded, not keeled (Text-fig. 26). The ascending arms are very thin, and will conform to the body contours in wrinkled specimens. This pelvic scute was noticed by Bertin (1943) in *Gilchristella* and *Sauvagella* and figured in the latter, but he referred to it as "*l'écaille verticale qui précède cette nagoire*". The arms of the scute lie below the scales and appear to be embedded in the skin.

In *Gilchristella aestuarius* alone there are also six to nine similarly spined, but slightly shorter scutes lying between the pectoral and pelvic fin bases (Text-fig. 27). All the specimens examined lacked a scute immediately in front of the pelvic scute. In no case were post-pelvic scutes present. These abdominal scutes are also rounded ventrally, not keeled. They are again very thin and are easily overlooked unless the specimen is stripped of scales and thoroughly dried.

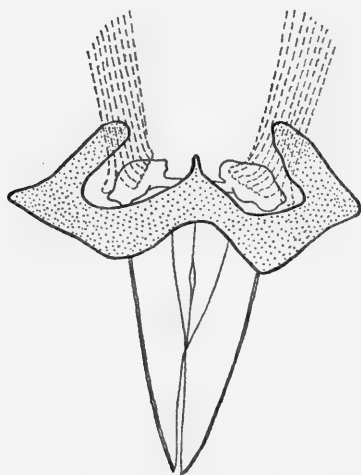


FIG. 25.

The w-shaped pelvic scute (stippled) in *Spratelloides delicatulus*. Ventral view, pelvic finrays shown by broken lines.

Previous records of abdominal scutes in the round herrings have all proved erroneous. Thus Fowler (1941) was correct to presume that the 9 pre-pelvic and 7 post-pelvic scutes shown by Sauvage (1891) for *Gilchristella madagascariensis* were an artist's error: the entire figure is a poor one and there are no such scutes in the types (see Bertin, 1943). The "hard sharp keel on the thoracic region in front of the pectorals" described by Barnard (1925) for *G. aestuarius* is not due to scutes,

but is the sharp keel formed by the ventrally apposed edges of the two coracoids ; it occurs in other species also. The scuted *Pellonulops* Smith was almost certainly based on a clupeid.

Taken in conjunction with other characters (especially numbers of branchiostegal rays) the "modified" w-shaped pelvic scute may perhaps be the primitive form from which fully scuted species have arisen. To some extent the variation in scute development in the round herrings resembles that of the anchovies, where, however, ventral scutes are more common. In the most widespread (and perhaps most

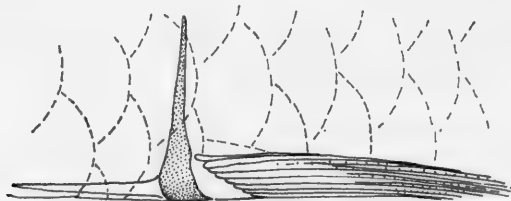


FIG. 26.

Left pelvic scute in *Ehirava malabaricus* (stippled) showing ascending lateral arm.

primitive) anchovy, *Engraulis encrasicolus* (and its allied forms in Australia, America and Japan) there is a single pelvic scute only, which is of the spined, *S. malabaricus* type. This is the case also in all the American anchovies. Of the more specialized anchovies of the Indo-Pacific region, species of *Stolephorus* have up to six or seven keeled scutes, each with a backwardly directed spine between the pectoral and pelvic bases ; *Thrissocles baelama* has both pre- and post-pelvic scutes ; and other species of *Thrissocles*, as well as *Setipinna*, have in addition a few scutes in front of the pectorals also. In the Clupeidae scutes always appear to be present both in front of and behind the pelvic fins. Engraulidae and Clupeidae both have the spined pelvic scute and it seems clear that the evolution of this pelvic scute preceded the evolution of the other abdominal scutes. The pelvic scute may perhaps be the most important functionally, possibly lending support to the pelvic fin ; thus in specimens from all three families I have found a small ligament arising from a point about half way along the posterior edge of the spine of the pelvic scute. This ligament is attached near the base of the outer (or upper) half of the first pelvic ray. It does not occur in those round herrings which have a w-shaped pelvic scute. The

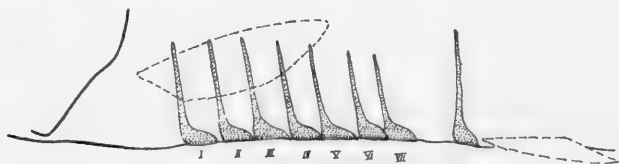


FIG. 27.

Pelvic, and seven pre-pelvic scutes (stippled) in *Gilchristella aestuarius*. Left lateral view. Pectoral and pelvic fins indicated by broken lines.

presence of the ligament suggests that the spined scute plays some role in the movements of the pelvic fins. The abdominal scutes, however, may have had a very different evolutionary history, although closely resembling the pelvic scute in their modern form.

Mention should be made of Chapman's (1944) belief that the abdominal scutes in the Engraulidae are derived from the ventral myorhabdoi (which occur from anus to caudal base in engraulids; and occur anterior to the anus but not behind it in clupeids). This author argued that the possession of ventral scutes is a primitive character in the clupeids "because of the theoretical necessity of the possession of ventral myorhabdoi by antecedent clupeoids"; he notes the absence of these myorhabdoi in the Dussumieriidae (i.e. in *Etrumeus*). Ontogenetic studies might support this view, but such a direction to scute evolution contradicts the evidence of several other characters, and especially that of branchiostegal ray number.

Upper and Lower Jaws

The lower jaw in the Dussumieriidae very closely resembles the lower jaw of the Clupeidae and there appear to be no consistent differences which could serve to separate the two on this character. It is worth noting that the lower jaw in the cretaceous *Clupavus* (i.e. *C. neocomiensis* (Bassani) figured by Arambourg, 1954) is also identical to the normal clupeid condition.

The upper jaw elements, although very similar in the two families, are generally narrower in the round herrings. In the Dussumieriinae in particular, the posterior supra-maxilla is not more than half as deep as the maxilla and in *Etrumeus* it is only about a quarter as deep (see Text-fig. 28d and e). In the Spratelloidinae the posterior supra-maxilla is more paddle-shaped, the expanded portion being equal to or a little deeper than the deepest part of the maxilla, but it is still a narrower bone than in the clupeids, being at least five times as long as deep (see Text-fig. 28a, b and f and compare with a fairly typical clupeid, *Harengula ovalis*, Text-fig. 28c).

A second, anterior supra-maxilla is present in some round herrings but not in others. In the Dussumieriinae, *Dussumieria* has a second supra-maxilla, but *Etrumeus* does not; in the Spratelloidinae this bone is present in *Spratelloides gracilis* and *S. delicatulus*, but is absent in the Ehiravini as well as in *Jenkinsia*. The importance of this little bone in the phylogeny of the group is questionable, but it is worth noting that amongst the Spratelloidinae it is consistently absent in the species with spined pelvic scutes, but present in fishes with w-shaped pelvic scutes (except *Jenkinsia*). When present, the second supra-maxilla is a thin and plate-like bone lying just below the anterior shaft of the first supra-maxilla. Its shape is somewhat variable.

The lower edge of the maxilla is in most dussumieriids fairly evenly rounded but in *E. malabaricus* it is excavated anteriorly as in some clupeids. The lower edge bears a single row of fine teeth along most of its length.

The premaxilla is a short and rather narrow bone in the Dussumieriidae. It bears teeth in both *Etrumeus* and *Dussumieria* but of the Spratelloidinae only *Jenkinsia lamprotaenia* and members of the Ehiravini have toothed premaxillae (species again

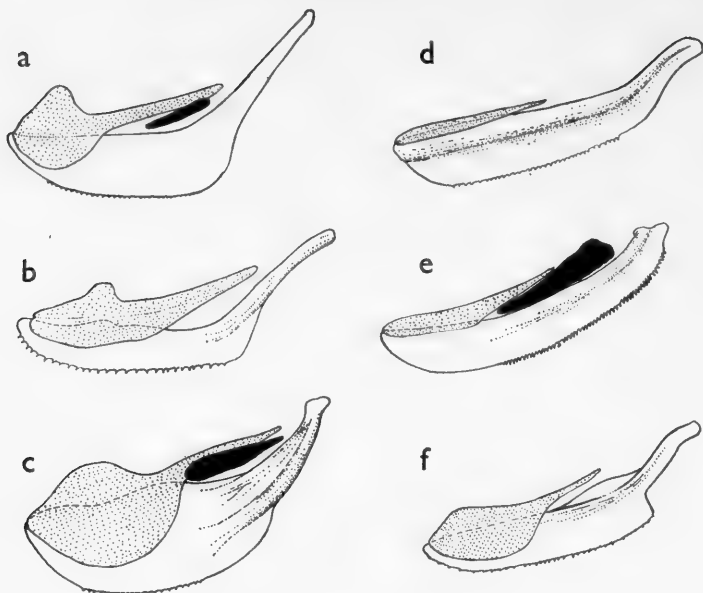


FIG. 28.

Upper jaw elements in species of round herring. Maxilla, plain; 1st (anterior) supra-maxilla, black; 2nd (posterior) supra-maxilla, stippled.

- a. *Spratelloides delicatulus* 41 mm.
- b. *Jenkinsia lamprotaenia* 34 mm.
- c. *Harengula ovalis* 112 mm. (Clupeidae).
- d. *Etrumeus teres* 88 mm.
- e. *Dussumieria acuta* 100 mm.
- f. *Ehirava malabaricus* 58 mm.

which lack a second supra-maxilla). The premaxillary teeth and the anterior supra-maxilla are probably primitive characters whose independent loss in some genera but not others is to be expected.

Branchiostegal Rays

A principle division between the *Spratelloidinae* and the *Dussumieriinae* can be made on numbers of branchiostegal rays (6-7 in the former, 14-20 in the latter). In both groups the rays are borne on the epi- and the ceratohyal. In the *Spratelloidinae* the ceratohyal is excavated ventrally at the head of each ray, as is the case in some (if not all) Clupeids (see Chapman *loc. cit.*), but in both *Etrumeus* and *Dussumieria* the lower edge of the ceratohyal is smooth (Text-fig. 29a-d). The individual rays, and especially the posterior ones, are broader in the *Spratelloidinae* than in the *Dussumieriinae*.

There seems little doubt that generally speaking, reduction in the number of branchiostegal rays in the clupeoid fishes has been a progressive evolutionary trend. It is therefore tempting to consider all other differences between the *Dussumieriinae*

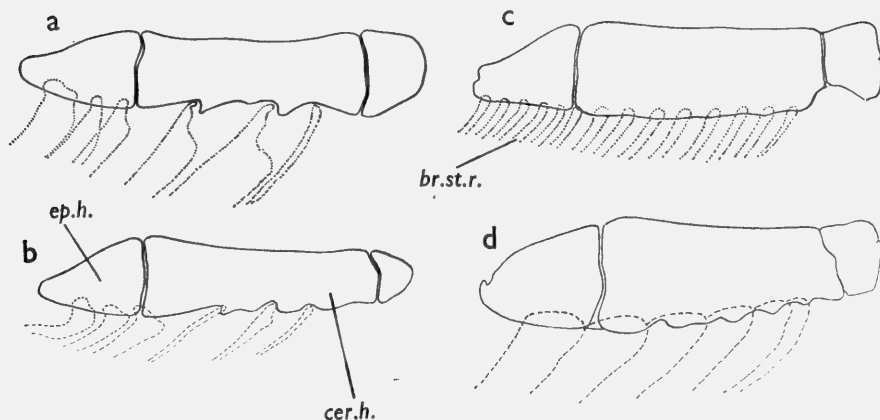


FIG. 29.

Hyoid bones and attachment of branchiostegal rays in species of round herring.

a. *Spratelloides delicatulus* 41 mm.

b. *Jenkinsia lamprotaenia* 34 mm.

c. *Dussumieria acuta* 100 mm.

d. *Gilchristella aestuarius* 53 mm.

ep.h. epihyal.

cer.h. ceratohyal.

br.st.r. branchiostegal rays.

and the *Spratelloidinae* as evidence of the primitiveness of the former, especially where a series (such as the development of the "cleithral flap") is concerned. Certainly the evidence of branchiostegal ray numbers suggests the direction of scute evolution, from a simple w-shaped pelvic scute to the spined scute and thus to the fully keeled scutes of the *Clupeidae*.

Shape of Gill Opening and Bones of Opercular Series

In the series *Etrumeus-Dussumieria-Spratelloides* there is a steady development of a flap of skin on the postero-ventral angle of the cleithrum (the cleithral flap) as shown in Text-fig. 30a-c. In *Etrumeus* the posterior angle of the gill opening is an approximate right-angle and there is usually no flap of skin. In *Dussumieria* the posterior angle is more acute and individuals show varying degrees of development of the flap. These two genera also differ in the posterior outline of the gill opening, from almost straight and vertical in *Etrumeus*, to curved in *Dussumieria*. In *Spratelloides* the flap of skin is raised markedly above the ventral line of the gill opening and is indented anteriorly, while the posterior outline of the gill opening is rather irregularly shaped, conforming to the indentation in the posterior margin of the operculum, especially in juvenile fishes.

It is rather difficult to see what function the "cleithral flap" serves. Where it is well developed, the ventral outline of the inter- and sub-opercular bones and the branchiostegal rays is indented; obviously, in order to seal the gill opening, one development necessitates the other, but it is difficult to determine which developed

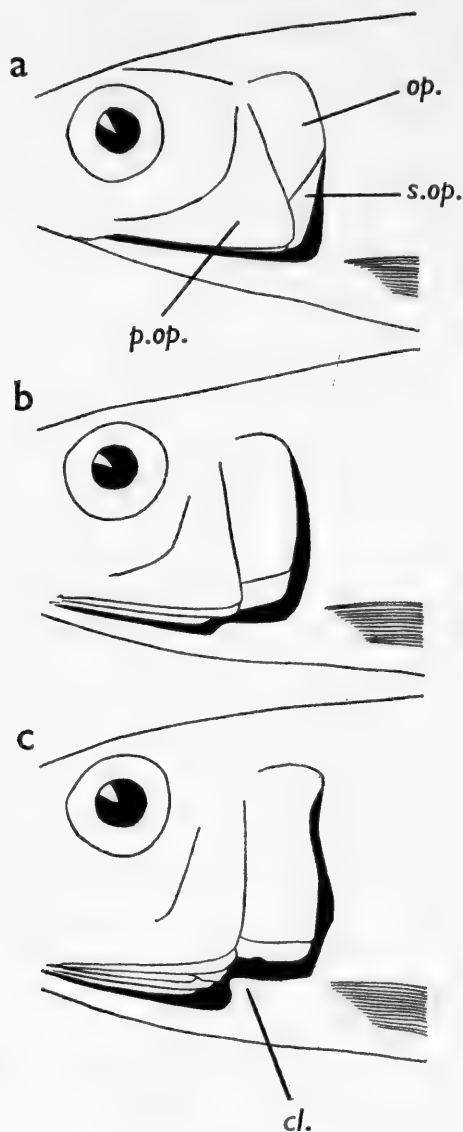


FIG. 30.

The shape of the posterior outline of the gill opening, and of the bones of the opercular series in the species of round herring. Gill cover slightly raised.

- a. *Etrumeus teres*.
- b. *Dussumieria acuta*.
- c. *Spratelloides delicatulus*.
- op. operculum.
- s.op. sub-operculum.
- p.op. pre-operculum.
- cl. "cleithral flap".

first. In *Etrumeus* the interoperculum and branchiostegal rays are barely visible from the outside ; in *Dussumieria* they are more obvious, at least one branchiostegal ray being visible ; in *Spratelloides* three or more branchiostegal rays can be seen, and the penultimate ray is expanded posteriorly. In addition, in *Spratelloides* the gill filaments of the first arch are indented round the cleithral flap.

In members of the tribe Ehiravini and in species of *Jenkinsia* the cleithral flap is very poorly developed, usually approximating to a condition intermediate between *Etrumeus* and *Dussumieria*. This is perhaps surprising since the Ehiravini are in other characters closer to *Spratelloides*. The shape of the operculum and suboperculum in the Ehiravini are also of the dussumieriine type, the angle between these two bones rising posteriorly, and not lying horizontally as in *Spratelloides*. The cleithral flap is well-developed in the clupeid genera *Harengula* and *Sardinella* among others and this is a further reason for expecting it to be large in the Ehiravini. As suggested later (p. 368), the Ehiravini must be considered a group which, although in several ways nearer to the Clupeidae than are the Spratelloidini, have none the less retained some primitive features reminiscent of the Dussumieriinae.

As in the development of the cleithral flap, so in the shape of the operculum and suboperculum a progressive change occurs between *Etrumeus* and *Spratelloides*, with *Dussumieria* occupying an intermediate position. The most obvious trend is in the angle of the line formed between the operculum and suboperculum. In *Etrumeus* (Text-fig. 30a) the lower edge of the operculum rises at a steep angle which, if projected, would meet the dorsal body profile some distance before the dorsal fin. The suboperculum is thus roughly triangular (with its apex pointing forwards). In *Dussumieria* (Text-fig. 30b) the lower opercular margin is nearer the horizontal and the suboperculum more rectangular. This trend is continued in *Spratelloides*, with a horizontal opercular margin and rectangular suboperculum (Text-fig. 30c).

Together with this change is a progressive deepening of the operculum, and its anterior border (i.e. junction with the preoperculum) becomes more vertical. The ascending limb of the preoperculum thus becomes more upright.

To some extent the *Etrumeus* condition can be equated with that found in the engraulids, and the *Spratelloides* condition to that found in the Clupeids. The resemblance is even more marked when the posterior margin of the operculum is also considered, for in *Harengula* at least, there is a tendency for the upper part of the margin to be excavated, with a corresponding bulge in the posterior gill opening profile. In *Spratelloides*, and especially in juveniles, this excavation of the operculum is most marked, but it does not occur in *Dussumieria* or *Etrumeus*.

Other Features of the Skull

The skull of *Dussumieria acuta* was described and figured by Ridewood (1904), who compared it with several other clupeoids. Chapman (1948) compared the osteology of *Etrumeus teres* with that of the clupeid *Sardinops caerulea* and found six principal differences, which were however shared with the Engraulidae. Some of these differences disappear if the Spratelloidinae are included (numerous branchiostegal rays, smooth lower edge of ceratohyal and lack of ventral scutes). Again, while *S. caerulea* has a single articular head to the hyomandibular, the Dussumieriidae

cannot be absolutely separated from the Clupeidae on this character since in *Alosa finta* at least there are two articular facets (Ridewood, *loc. cit.*, fig. 124).

A major difference between the Dussumieriinae and the Spratelloidinae is the retention in adults of the latter of a pair of fontanelles immediately in front of the supra-occipital. These have been referred to here as the posterior fontanelles, and are shown in Text-figs. 31 and 32. They are bounded anteriorly and laterally by the frontals, and are divided in the midline by a narrow median extension of the supra-occipital, which also forms the posterior margin of the fontanelles.

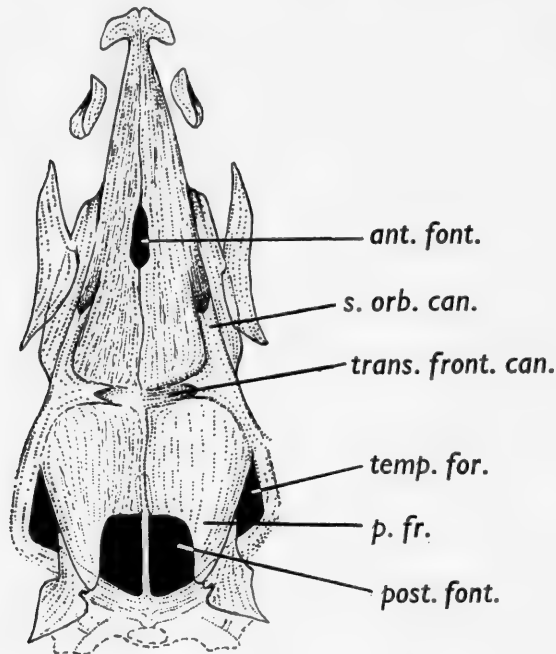


FIG. 31.

Spratelloides delicatulus, dorsal view of cranium showing the anterior and posterior fontanelles and the temporal foramen. From an alizarin stained specimen of 40 mm.

- ant. font.* anterior fontanelle.
- s. orb. can.* supra-orbital canal.
- trans. front. can.* transverse frontal canal.
- temp. for.* temporal foramen.
- p. fr.* posterior extension of the frontals.
- post. font.* posterior fontanelle.

No such fontanelles are present in the adults of *Dussumieria* or *Etrumeus*, but in a juvenile of *Dussumieria* of 49 mm. the fontanelles were present and together comprised an area equal to the pupil of the eye.

As has already been pointed out (see p. 349) the form of the fontanelles and of the posterior part of the two frontals is different in the two species of *Jenkinsia*, one resembling the condition found in *Spratelloides* and the other that in the Ehiravini.

Thus in *J. majua* and in species of *Spratelloides*, the posterior median portion of the frontals, while forming a small wedge between the two fontanelles, is not depressed into a shallow triangular hollow, but in juveniles is domed.

In both types of fontanelle formation, the length of the fontanelles decreases with the size of the fish, but more so in *J. lamprotaenia* and the Ehiravini. In large specimens of *Ehirava malabaricus* (of about 60 mm.) the fontanelles are barely apparent. This suggests that the second type of fontanelle formation (i.e. those which are broadly divided anteriorly) is the more primitive of the two. In this respect *J. lamprotaenia* and the Ehiravini show greater affinities with the Dussumieriinae than do species of *Spratelloides* or *J. majua*.

In both the Spratelloidinae and the Dussumieriinae there is a transverse commissure linking the supra-orbital sensory canals a little behind the centre of the orbits (see Text-fig. 32). This has been referred to here as the transverse frontal canal

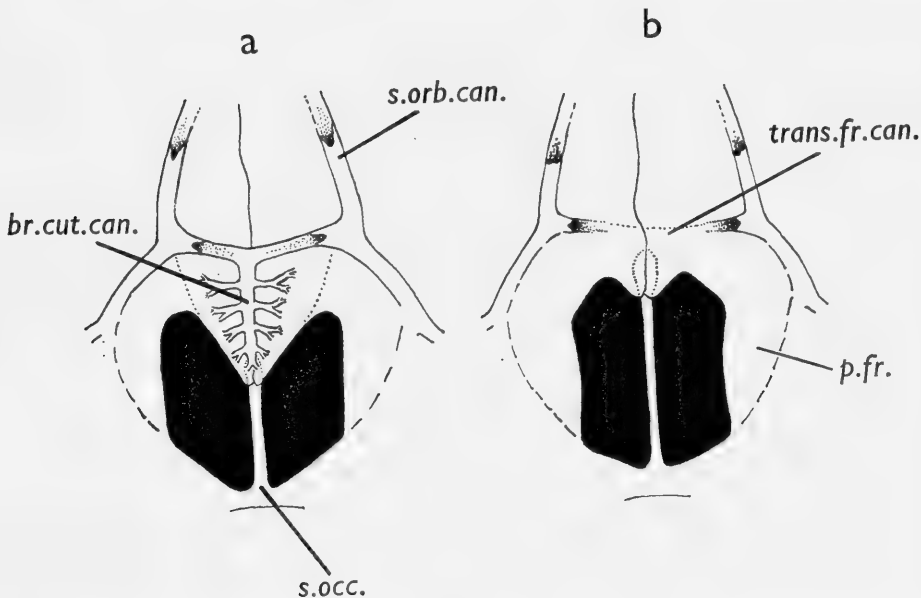


FIG. 32.

Two types of posterior fontanelle (black) found in members of the Spratelloidinae. Dorsal view of head with skin removed to expose fontanelles.

a. *Jenkinisia lamprotaenia* (at 35 mm.) showing large wedge of bone (part of frontals) dividing anterior part of fontanelles. Within the depressed area of this wedge lies a branched, cutaneous sensory canal.

b. *Jenkinisia majua* (at 40 mm.) showing posterior fontanelles only narrowly divided and with no cutaneous sensory canal.

s. orb. can. supra-orbital canal.

p. fr. posterior extension of the frontals.

trans. fr. can. transverse frontal canal.

s. occ. supra-occipital.

br. cut. can. branched cutaneous canal lying in triangular depression.

(the epiphysial canal of Weitzman, 1962). The central part of this canal is cutaneous and not roofed over with bone. Extending posteriorly from this canal there is, in certain dussumieriids, a branched cutaneous canal which reaches to the apex of the triangular depression mentioned earlier. This is found in the Dussumieriinae, in the Ehiravini, and in *Jenkinsia lamprotaenia*, i.e. in those fishes which have a pronounced triangular depression behind the transverse frontal canal. In *J. lamprotaenia* and the Ehiravini this triangular depression is most marked; it also closely resembles the condition found in juvenile *D. acuta*. In adult dussumieriines the triangular depression reaches to the posterior border of the skull, the fontanelles having been occluded by posterior growth of the frontals.

Although the posterior branch leading from the transverse frontal canal appears to be usually absent in those fishes in which the triangular depression is either poorly developed or absent, there is a small canal in large specimens of *Spratelloides*. The triangular depression and its relationship to the cephalic canals was recently mentioned by Gunter & Demoran (1961) in dealing with the Gulf Menhaden (*Brevoortia patronus*); they comment on the absence in the literature of any description of this part of the cephalic sensory system, and they refer to it as the "cephalic spongy sensory area".

The lateral edges of the triangular depression are usually well-defined. In some dorosomatids and clupeids these lateral edges are wedge-shaped and bear a few or many longitudinal striae (see Whitehead, 1962b) but this is only faintly apparent in the dussumieriids (i.e. in *Dussumieria*).

SPECIATION IN THE DUSSUMIERIIDAE

The round herrings are an old group, with a lineage extending back at least to Cretaceous times (if *Clupavus* is to be accepted as a dussumieriid). It is not surprising therefore to find a number of fairly well defined genera which can be clearly separated on osteological grounds. But intrageneric variation is usually small and I have here recognized one or at most two species only per genus, although in some cases the species can then be subdivided into subspecies. The situation is however, one in which the museum worker must decide in a rather arbitrary manner where the boundary between species and subspecies and demes should lie.

If subspecies are defined as geographically isolated members of an interbreeding population which differ consistently in at least one character from the rest of the population, then there is a case for subdividing the forms of *Dussumieria*. But, as already pointed out, the geographically and morphologically intermediate forms so effectively bridge the gap between the extremes that no practical boundaries can be drawn. There is thus reason to suppose that populations of *D. acuta* in China and the Red Sea are reproductively linked, however tenuous that link may be.

In the case of forms which are distinct from each other but whose geographical ranges overlap (e.g. in the two species of *Spratelloides* or *Jenkinsia*) there seems good reason to believe the two forms to be separate species. But where the geographical ranges do not overlap (as in *Etrumeus*) it would seem that the probable value (or weight) of each particular morphological character must be assessed. Thus in *Etrumeus* the differences between populations are small and are of the same order

as those found in populations of *Dussumieria*. In only a single case (the South African population of *Etrumeus*) is there a clear-cut difference. But since this rests solely on a single dorsal ray, it would be unrealistic to consider this of specific value in view of the degree of variation in the rest of the genus.

Since there is as yet no generally applicable criterion of a bio-species other than that it is reproductively isolated from its nearest relatives, the conclusions reached in the museum must contain an element of guesswork. Thus the present classification provides a framework, the details of which will no doubt be altered as larger collections become available.

ORIGIN AND RELATIONSHIPS OF THE ROUND HERRINGS

In attempting to work out a probable phylogeny of the Dussumieriidae and their relationship to the Clupeidae, it is possible to suggest morphological series for several characters. The most obvious and perhaps most reliable trend is the reduction in numbers of branchiostegal rays, with the Dussumieriinae the most primitive and the Spratelloidinae the most advanced. If this is accepted, then it is difficult not to correlate with it scute development, the w-shaped pelvic scute being the most primitive, and the scutes of *Gilchristella aestuarius* being the most advanced form in the Dussumieriidae as a whole. From *G. aestuarius* a fully scuted and keeled clupeid is a logical development. In the shape of the gill opening, the development of the cleithral flap, and the shape of the bones in the opercular series, there is a good transition from *Etrumeus*, through *Dussumieria* to *Spratelloides* (see Text-fig. 30a, b, c), and since these trends also coincide with those of branchiostegal rays and scutes, it would seem at first sight as if the Ehiravini need only be added to the series to make a perfect development through to the Clupeidae. But although the Ehiravini complete the trend in scute development (and compression of the body), and in addition complete also the trends for advance of the pelvics and increase in length of anal, yet in other respects they more closely resemble the Dussumieriinae. Thus the cleithral flap is small, the suboperculum is more nearly triangular, the lower edge of the operculum is less horizontal and the premaxillae bear teeth. But if scute development is a progressive trend, then the place of the Ehiravini seems to be between the Spratelloidinae and the Clupeidae.

Also anomalous in some respects is *Jenkinsia*. Whereas *J. majua* could be placed with *Spratelloides* but for the absence of an anterior supra-maxilla, *J. lamprotaenia* shares with the Ehiravini a toothed premaxilla and a similar shape and development of the posterior fontanelles. Both species however lack the large cleithral flap of *Spratelloides* and thus resemble the Ehiravini. Most likely *Jenkinsia* represents a form which existed before both *Spratelloides* and the Ehiravini diverged fully. Because of its isolation, *Jenkinsia* may still retain early characters which have become lost or modified in *Spratelloides* and the Ehiravini.

The scutes of *G. aestuarius* and the split anal of *S. bianalis* foreshadow trends which become more fully elaborated in the clupeids. In the Ehiravini they probably represent tentative developments which have no adaptive value but which have remained and indicate the type of experiment prevalent amongst ancestors of the modern Clupeidae.

If the phylogeny of the Dussumieriidae and the Clupeidae were to be represented diagrammatically, it would probably be correct in a general way to show the Clupeidae branching from near the split between the Ehiravini and the Spratelloidini, and the latter diverging initially from the Dussumieriinae (Text-fig. 33). Since all these forms have a lower jaw so very different from the long jaw of the Engraulidae (and in addition lack the prominent mesethmoid typical of the anchovies), it seems

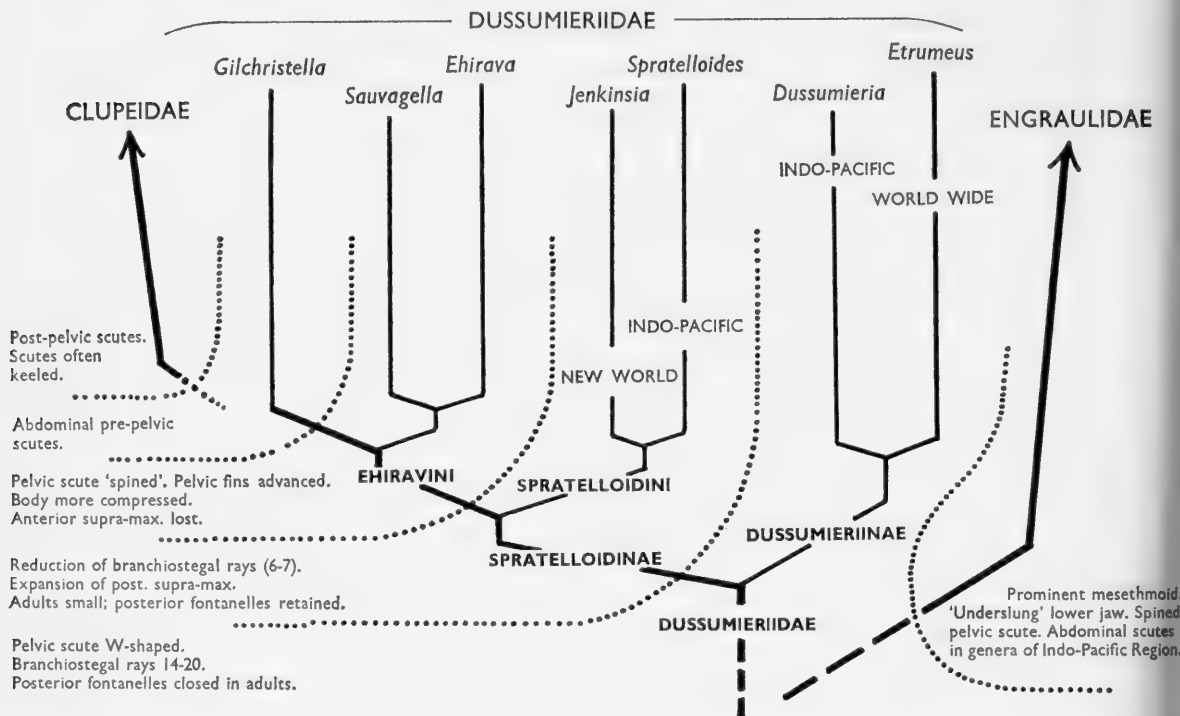


FIG. 33.

A possible phylogeny for the round herrings, indicating stages in the development of certain clupeid-like characters. For further explanation, see text.

reasonable to suggest that, not only did the Engraulidae diverge from the main stem (primitive round herrings) before the Clupeidae did, but that in the Engraulidae the initial trend at least was one of scute development, not degeneration (cf. Jordan & Seale, 1926). Against the proposition that the Engraulidae evolved from a scuted clupeid-like ancestor is the high number of branchiostegal rays in the Engraulidae and the other osteological resemblances which Chapman (1948) found between the anchovies and the Dussumieriinae.

Jordan & Seale (1926) thought an independent development of scutes in both anchovies and herrings unlikely. But in *Engraulis encrasicolus* there is a single pelvic scute only, of the spined type, and as the Ehiravini show, a fully scuted form can be derived from this. Early engraulids may have had a w-shaped pelvic scute,

although it is possible that in the Dussumieriinae and Spratelloidini this type of scute is a degeneration from the spined scute. This possibility, and the implication that the Spratelloidini might have branched off from the Dussumieriinae *after* the Ehiravini had also diverged from the Dussumieriinae, would help to explain the similarities shown by the Ehiravini to the Dussumieriinae rather than to the Spratelloidini. But it also implies the independent reduction of branchiostegal rays in both Ehiravini and Spratelloidini and the parallel evolution of other similarities between these two tribes (small adult size, retention of post-frontal fontanelles, broad posterior supra-maxilla). It seems more likely that the w-shaped pelvic scute marks a step in the evolution of scutes, not a modification, but that it is no longer found in the Engraulidae.

Two further aspects of scute evolution must be mentioned. A striking feature in the present study has been the very constant presence of the pelvic scute, not only in the Dussumieriidae, but in otherwise non-scuted engraulid genera (i.e. in *Engraulis*), as well as in the clupeids. There remains the possibility that this scute has evolved from the pelvic splint bones which are found in some fishes (see Gosline, 1961). Such an evolution demands the expansion of the base of the splint to form either a w-shaped plate or an ascending arm, and at the same time the degeneration of the splint itself (which normally extends along the outer face of the first pelvic ray). Such a development is at least a possibility since splint bones are not present in the Dussumieriidae, Clupeidae or Engraulidae, but occur in certain other lower teleosts (*Tarpon*, *Chanos*, *Salmo*—see Gosline, 1961).

The second aspect of scute evolution is the question whether scutes could have evolved quite simply from the median series of abdominal scales without the prior evolution of the pelvic scute. Thus in *Denticeps clupeoides*, the only extant member of the family Denticipitidae (Clausen, 1959), pre- and post-pelvic abdominal scutes are present, but there are no pelvic scutes comparable to the pelvic scutes of the clupeids, engraulids or dussumieriids. However, the scutes in *Denticeps* are clearly the median series of scales which have become sharply folded in the midline and have developed posterior spines. In appearance they strongly resemble the spiny scutes of the engraulids (e.g. *Stolephorus*) but they differ in one important respect: they have no ascending arms, but are rounded laterally like a scale. The presence of ascending arms in the three clupeoid families discussed here and the constancy of the pelvic scute, seem to indicate that the evolution of the clupeoid scutes was in some manner linked to the evolution of the pelvic scute, and that the evolution of the scutes in *Denticeps* has followed a rather different course; it may be significant that the latter has no pelvic splint bones.

The fossil evidence throws a certain amount of light on the problem, but branchiostegal counts have never been certain and the descriptions are not always adequate to decide whether a dussumieriine or a spratelloidine is involved.

The earliest record of a round herring is probably *Clupavus neocomiensis* (Bassani). Arambourg (1954) placed specimens from the Cretaceous of Morocco in the Dussumieriidae because of their absence of scutes. His figures of the head (figs. 14 and 16) very much resemble *Etrumeus*, especially in the shape of the opercular series, but vertebral numbers (39 or 40) are more those of a modern spratelloidine. Un-

fortunately exact branchiostegal counts were not possible, but there were probably not more than twelve.

The importance of *Clupavus* lies in the links which Arambourg (1950 and 1954) believed that it showed with the primitive actinopterygians (palaeoniscids, holosteans and halecostomes). These were principally in the large parietals, which meet in the midline, and the presence of a pair of posteriorly directed canals branching from the supra-orbital canals and converging across the posterior parts of the frontals (but not meeting each other). But from the position and size of the large parietals, it is tempting to suppose that they are, at least in part, the posterior fontanelles typically found in small round herrings. This would explain the rather abrupt termination of the frontal sensory canal at the border between the frontals and the parietals. In the specimen figured by Arambourg (1954, fig. 15 and pl. 3, fig. 4) much of the median part of both parietals is missing, as also is an area between the anterior ends of the frontals. The latter almost exactly corresponds in shape and position to the normal anterior fontanelle of round herrings. *Clupavus neocomiensis*, as Arambourg recognized, is in many respects very clupeid-like, and such large parietals meeting in the midline seem unlikely. In the round herrings the parietals are fairly small and are well separated (see Text-fig. 31).

With regard to the sensory canal system, in the modern round herrings there is no frontal branch similar to that found in *Clupavus*. However, Arambourg (1950 and 1954) was mistaken in believing that *Clupavus* is unique amongst the teleosts in possessing such a frontal branch. While it may well be absent in the higher teleosts, it is certainly present in the characid genus *Brycon* (the parietal canal in Weitzman, 1962), and Dr. P. H. Greenwood has shown me a short but well-formed canal in the problematical *Denticeps*.

Arambourg (1954) also makes the important observation that differentiation within the clupeoid fishes was well-established by the beginning of the Cretaceous and he mentions the coexistence amongst others of *Parachanos*, *Clupavus* and *Diplomystus*. Presumably the Engraulidae had evolved by this time.

In Text-fig. 33 is shown a possible phylogeny of the round herrings with indications of the points at which particular characters first appear. As discussed above, the Ehiravini are difficult to place in any such scheme because they share characters both with the Spratelloidini and with the Dussumieriinae as well as with the Clupeidae. Thus the diagram presents one of several possible schemes, but the one which appears to involve the least number of contradictions. Whatever scheme is adopted, the independent loss of one or more characters in genera which are not closely related must be assumed.

It is also important to decide which features are primitive and which specialized. Thus *Dussumieria* differs from *Etrumeus* in having two supra-maxillae and more advanced pelvics, but *Etrumeus* only is represented in the fossil record (see Bertin, 1943, Arambourg, 1945). On the other hand, *Leptolepis* as well as the more primitive isospondyls such as *Elops* or *Albula*, all have rather advanced pelvics and two supra-maxillae (except *Albula* with one). Thus *Dussumieria* may in fact be the more primitive of the two. Unfortunately other fossil genera referred to the Dussumieriidae (*Lygisma*, *Quaesita* and *Sternbergia*) are either inadequately described or too

poorly preserved to be of any value in determining which characters are more primitive. But if the Dussumieriinae as a whole are considered more ancient than the Spratelloidinae, then the following characters must be considered primitive: pre-maxillary teeth, two supra-maxillae (the posterior rather narrow), a small cleithral flap, pelvics set below or perhaps in front of the dorsal (the evidence here is however equivocal), post-frontal fontanelles not retained in the adult (but present possibly in *Clupavus*), suboperculum triangular, scutes absent or represented only by a w-shaped pelvic scute, anal fin fairly short.

The possibility that primitive forms were scuted has been discussed on pp. 356-359. This depends largely on whether the ventral myorhabdoi are in fact homologous with the ventral scutes. Although such an interpretation would certainly explain the resemblance shown by the Ehiravini to the Dussumieriinae, it would presuppose the independent degeneration of the pelvic spined scute to a w-shaped scute in the Spratelloidinae as well as the Dussumieriinae, and would involve several other parallel specializations or losses, as already mentioned. It seems more likely on present evidence that the round herrings are modern representatives of an early non-scuted herring.

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It gives me great pleasure to record the assistance which I have received from other museums and institutions, and their willingness to lend or donate specimens; to the individuals concerned go my sincere thanks. I also wish to thank Professor Carl L. Hubbs for stimulating the search for the correct name for *Etrumeus teres* and for allowing me to use some of his unpublished data; Mr. N. B. Marshall for commenting on the text; and Dr. P. H. Greenwood for his most generous help with certain systematic problems, much useful discussion, and many valuable criticisms of the text.

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- (In press.) The true identity of *Clupea sadina* Mitchell, 1814. *Copeia*.

STUDY MATERIAL

The first name is that which is used in this paper ; the second (in parenthesis), that under which the specimens have been labelled hitherto.

Dussumieria acuta

(*D. acuta*)

6 fishes, 121-148 mm., Shihr & Burum, Gulf of Aden (1962.3.26.211-216¹).

(*D. acuta*)

5 fishes, 105-114 mm., Mukalla, Gulf of Aden (1962.3.26.217-221).

14 fishes, 105-120 mm., Singapore (1935.4.12.3-12).

1 fish, 114 mm., Andamans (1889.2.1.2047).

1 fish, 122 mm., Bombay (1889.2.1.2037).

¹ British Museum registration numbers unless stated otherwise.

(D. acuta)-contd.

- 4 fishes, 93-141 mm., Madras (1889.2.1.2042-5).
- 1 fish, 118 mm., Borneo (1868.1.28.81).
- 1 fish, 98 mm., Port Blair (1889.2.1.2046).
- 1 fish, 94 mm., locality unknown (1860.3.19.956).
- 2 fishes, 106-107 mm., Djambi, Sumatra (1934.8.18.12.13).
- 3 fishes, 69-84 mm., Malabar (1889.2.1.2039-41).
- 5 fishes, 82-119 mm., Batavia (1934.8.18.17-19).
- 5 fishes, 92-100 mm., Panci Sumatra (1934.8.18.14-16).
- 5 fishes, 89-100 mm., Batavia (1934.8.18.20-22).
- 5 fishes, 64-114 mm., Haifa, Israel (1962.6.13.4-8).
- 1 fish, 48 mm., Malabar (1889.2.1.2049).
- 20 fishes, 77-107 mm., Haifa, Israel (Sea Fisheries Research Station (Israel) collection).

(D. elopsoides)

- HOLOTYPE, 124 mm., Madura (1867.11.28.17).
- 1 fish, 116 mm., Zool. Soc. Coll. (1852.9.13).
- 1 fish, 88 mm., Amboina (1858.4.21.360).
- 2 fishes, 114-115 mm., Siam (1920.7.13.4-5).
- 1 fish, 101 mm., Amoy, China (1860.7.20.88).
- 12 fishes, 107-115 mm., Calicut (1935.9.20.1-8).
- 1 fish, 118 mm., Foochow (1936.10.7.21).
- 1 fish, 113 mm., Hong Kong (1939.3.23.5).

(D. hasselti)

- HOLOTYPE, 134 mm., Java 1867.11.28.21).
- 3 fishes, 85-88 mm., Coromandel (types of *D. acuta*, Paris Museum, No. 3694).
- 9 fishes, 68-120 mm., Malabar (types of *D. acuta*, Paris Museum, No. 3217).
- 4 fishes, 112-131 mm., Coromandel (types of *D. acuta*, Paris Museum, No. 3697).
- 3 fishes, 89-110 mm., Persian Gulf (coll. Blegvad. Univ. Zool. Mus., Denmark, No. CN 5-7).

Etrumeus teres*(E. teres)*

- 9 fishes, 115-130 mm., Woods Hole, U.S.A. (1934.11.30.1-9).
- 1 fish, 120 mm. approx. (*skeleton*), Woods Hole, U.S.A. (1934.11.30.10).

(E. micropus)

- 87 fishes, 67-78 mm., Nagasaki (1923.2.26.73-82).
- 1 fish, 136 mm., Kobe, Japan (1907.12.23.91).
- 1 fish, 85 mm., Hong Kong (1939.3.23.6).
- 1 fish, 126 mm., Japan (1867.11.28.265).
- 1 fish, 165 mm., Haifa (Sea Fish. Res. Sta. (Israel) collection).
- 8 fishes, 117-149 mm., Natal (1903.2.6.11-17).
- 2 fishes, 133-134 mm., Eilat, Red Sea (Sea Fish. Res. Sta. (Israel) collection).

(E. jacksoniensis)

- 2 fishes, 105-122 mm., Botany Bay (1897.10.27.49-50).

(E. acuminatus)

- 1 fish (HOLOTYPE of *Perkinsia othonops*), 265 mm., California (1891.5.19.210).
- 7 fishes, 109-125 mm., California (1962.6.13.9-15).
- 1 fish, 120 mm. approx. (*skeleton*), California (1962.6.13.16).

Ehirava malabaricus*(E. fluviatilis)*

- 1 fish (HOLOTYPE of *E. fluviatilis*), 48 mm., Ceylon (1929.7.1.1).
13 fishes, 30-46 mm., Ceylon (1929.7.1.2-9).

(Spratelloides malabaricus)

- 4 fishes, 46-56 mm., Canara (1889.2.1.2052-5).
1 fish, 40 mm., Malabar (1889.2.1.2048).
1 fish, 53 mm. (*skeleton*), Malabar (1889.2.1.2050).

Ehirava madagascariensis

- 1 fish (TYPE of *Spratelloides madagascariensis*), 40 mm., Madagascar. (On loan from Paris Museum, No. 3794).
10 fishes, 41.0-52.5 mm., Buffalo river, Cape Province (1878.1.22.33-43).
1 fish, 52 mm., Buffalo river, Cape Province (1878.1.22.25).

Gilchristella aestuarius*(Spratelloides aestuarius)*

- 1 fish, 51 mm., Durban (1915.7.6.3).
1 fish, 53 mm., Durban (1919.9.12.3).
1 fish, 53 mm., Milnerton lagoon, S. Africa.¹
1 fish, 45 mm., Knyssa, S. Africa.¹
1 fish, 40 mm., St. Lucia, S. Africa.¹
1 fish, 35 mm., Swartkops river, S. Africa.¹
2 fishes, 42-44 mm., East London, S. Africa (1962.6.13.2 and 3).²
1 fish, 39 mm., Kei mouth, S. Africa (1962.6.13.1).²
1 fish, 58 mm., Buffalo river, Cape Province (1878.1.22.24).

(Spratelloides sp.)

- 4 fishes, 37-41 mm., Swartkops river, S. Africa (1905.1.7.1-4).

(Clupea sagax)

- 3 fishes, 28-45 mm., Swartkops river, S. Africa (1898.12.17.9-11).

Sauvagella bianalis*(Spratellomorpha bianalis)*

- 5 fishes, 44-45 mm., Madagascar (TYPES of *Sauvagella bianalis* Bertin, Paris Museum, No. A 5174).

Spratelloides gracilis gracilis*(Spratelloides gracilis)*

- 1 fish (TYPE of *Clupea argyrotaenia* Bleeker), 66 mm., E. Ind. Arch. (1867.11.28.17).
3 fishes, 68-72 mm., Japan (4.46.8134).
4 fishes, 66-79 mm., Goto I., Japan (1907.12.23.96-9).
Many fishes, 52-83 mm., Nagasaki (1923.2.26.31-40).
Many fishes, 88-93 mm., Wakanoura, Japan (1923.2.26.41-50).
3 fishes, 56-66 mm., Formosa (1934.8.18.1-3).
2 fishes, 45-47 mm., Ghardaqa, Red Sea (1935.9.30.10-11).
Many fishes, post-larvae to 37 mm., Senafir, Gulf Aqaba (1951.1.16.36-60).
3 fishes, 47-48 mm., Sumatra (1934.8.18.9-11).

¹ On loan from Prof. J. L. B. Smith.

² Donated by Prof. J. L. B. Smith.

Spratelloides delicatulus delicatulus*(Spratelloides delicatulus)*

- 5 fishes, 53–70 mm., Hasler collection (1855.9.19.1153–58).
- 1 fish, 51 mm., Bonham I. (1874.11.19.65).
- 1 fish, 65 mm., purchd. of Dr. Bleeker (1869.11.28.34).
- 1 fish, 77 mm., Australia (1851.2.20.14).
- 1 fish, 28 mm., Kosi Bay, Zululand (1906.11.19.27).
- 29 fishes, 37–44 mm., Seychelles (1927.4.14.13–22).
- 5 fishes, 50–53 mm., Thousand Is. (1934.8.18.4–8).
- 15 fishes, 28–35 mm., Sulu Prov., Philippines (1933.3.11.25–34).
- 10 fishes, 21–49 mm., Firaun I., Gulf of Aqaba (1951.1.16.14–23).
- 12 fishes, 42–47 mm., Senafir, Gulf of Aqaba (1951.1.16.24–35).
- 22 fishes, 27–35 mm., Cocos-Keeling (1949.1.29.5–26).
- 16 fishes, 16–45 mm., Marsa Halaib, Red Sea (1960.3.15.16–31).
- 8 fishes, 36–39 mm., Kad Eidwid reefs, Red Sea (1960.3.15.33–39).
- 2 fishes, 49–52 mm., G'an, Maldives (1962.1.22.2–3).
- 16 fishes, 39–42 mm., Gulf of Aden (1962.6.19.1–16).
- 1 fish, 40 mm., alizarin preparation, Marsa Halaib, Red Sea (1960.3.15.32).

Spratelloides delicatulus robustus*(Spratelloides robustus)*

- 5 fishes, 33–68 mm., Port Jackson (1897.10.27.43–47).
- 81 fishes, 46–74 mm., coast of N.S.W. (1924.4.30.1–10).

Jenkinsia lamprotaenia lamprotaenia*(Dussumieria stolidifera)*

- SYNTYPES, 15 fishes, 30–36 mm., Key West, Florida (1884.7.7.47–56).

(Jenkinsia lamprotaenia)

- SYNTYPES,¹ 2 fishes, 53–56 mm., Jamaica (1962.7.19.3–4).

(Dussumieria lamprotaenia)

- 5 fishes, 19–22 mm., Cayman Island (1939.5.12.6–9).

(Jenkinsia lamprotaenia)

- 52 fishes, 48–53 mm., Cat Cay, Bahamas (1962.7.21.1–50; *ex*² U.M.M.L. 2317).
- 15 fishes, 25–36 mm., Cat Cay, Bahamas (1962.7.21.101–115; *ex*² U.M.M.L. 5066).
- 25 fishes, 25–30 mm., St. John, Virgin Islands (1962.7.21.121–145; *ex*² U.M.M.L. 5280).
- 5 fishes, 38–44 mm., St. John, Virgin Islands (1962.7.21.116–120; *ex*² U.M.M.L. 5278).
- 50 fishes, 33–38 mm., Monroe County, Florida (1962.7.21.51–100; *ex*² U.M.M.L. 6742).
- 19 fishes, 39–59 mm., Caribbean (20° 12' N; 91° 59' W) (1962.8.1.1–19; *ex*³ C.N.H.M. 66009).
- 6 fishes, 33–39 mm., Tom Owen Cay, British Honduras (1962.8.1.20–25; *ex*³ C.N.H.M. 50028).
- 22 fishes, 33–45 mm., Belize, British Honduras (1962.8.1.26–47; *ex*³ C.N.H.M. 9831).
- 25 fishes, 24–32 mm., Golfo Batabano, Cuba (1962.8.1.48–72; *ex*³ C.N.H.M. 61363).
- 8 fishes, 42–46 mm., off Dry Tortugas (1962.8.1.73–80; *ex*³ C.N.H.M. 61365).
- 21 fishes, 23–40 mm., Serrana Rock, Caribbean (1962.8.1.81–101; *ex*³ C.N.H.M. 66012).
- 6 fishes, 23–51 mm., Alacran Rock, Gulf of Campeche (1962.8.1.102–107; *ex*³ C.N.H.M. 66010).
- 19 fishes, 27–45 mm., Alacran Rock, Gulf of Campeche (1962.8.1.108–126; *ex*³ C.N.H.M. 61366).

¹ Stated by Günther (1868) to be two typical specimens from Gosse's collection.

² Donated by Prof. C. Robins from the collections of the University of Miami Marine Laboratory.

³ Donated by Dr. Loren Woods from the collections of the Chicago Natural History Museum.

Jenkinsia majua majua

- 1 fish, HOLOTYPE, 53.8 mm., Arcas Cay, Campeche Bank (U.S. Nat. Mus., No. 197412).
52 fishes, 25–53 mm., PARATYPES, Arcas Cay, Campeche Bank (Chicago Nat. Hist. Mus. No. 61362).
20 fishes, 45–55 mm., PARATYPES, Arcas Cay, Campeche Bank (1962.8.1.152–171; *ex*⁴ C.N.H.M., No. 66007).
2 fishes, 54 mm., PARATYPES (alizarin) Arcas Cay, Campeche Bank (Chicago Nat. Hist. Mus. No. 66008).
10 fishes, 46–54 mm., PARATYPES, Campeche Banks (1962.7.21.146–155).
25 fishes, 40–44 mm., PARATYPES, Arcas Cay, Campeche Bank (1962.8.1.127–151; *ex*⁴ C.N.H.M. 46265).

Jenkinsia majua woodsi

- 1 fish, 48 mm., HOLOTYPE, Nr. Quita Sueno Bank, Caribbean (U.S. Nat. Mus. No. 197413; *ex*⁴ C.N.H.M., No. 66011).
16 fishes, 40–46 mm., PARATYPES, Nr. Quita Sueno Bank, Caribbean (1962.8.1.173–188; *ex*⁴ C.N.H.M. 66011).
10 fishes, 36–46 mm., PARATYPES, Nr. Quita Sueno Bank, Caribbean (C.N.H.M. 66011).
25 fishes, 31–43 mm., PARATYPES, Nr. Swan I., Caribbean (U.S. Nat. Mus. No. 197413; *ex*⁴ C.N.H.M., No. 66013).
6 fishes, 29–48 mm., PARATYPES, Swan I., Caribbean (1962.7.21.181–186; *ex*⁴ C.N.H.M.—no number).
25 fishes, 28–39 mm., PARATYPES, Gun Cay, Bahamas (1962.7.21.156–180; *ex*⁴ U.M.M.L., No. 2102).

⁴ Donated by Dr. Loren Woods from the collections of the Chicago Natural History Museum.

TABLE I.—*A Comparison of Proportional and other Measurements of the Holotypes of Dussumieria hasselti and D. elopsoides*

		<i>D. hasselti</i>	<i>D. elopsoides</i>
Standard length	134.0 mm.	124.0 mm.
In % of S.L.			
Body depth	20.9	20.8
Head length	26.4	26.9
Snout length	9.0	8.8
Eye diameter	6.7	7.1
Post-orbital	10.1	9.2
Inter-orbital	5.8	5.6
(above eye centre)			
Snout to maxillary tip	8.9	8.7
Lower jaw length	12.3	12.4
Operculum height	11.2	11.3
Peduncle depth	8.2	8.8
Pre-dorsal distance	59.0	55.0
Pre-pelvic distance	65.0	64.5
Longest gillraker on 1st arch	3.4	3.5
<hr/>			
Gillraker count	22	23
Dorsal rays : simple	iv	iv
branched	16	17
Anal rays : simple	iii	iii
branched	13	13
Branchiostegal rays	17	15

TABLE II.—*Proportional Measurements, Expressed as Percentages of Standard Length, for Specimens of Etrumeus from Five Regions*

	N. American Atlantic	Japan and Hong Kong	N. American Pacific	Australia	Natal, P. Elizabeth (South Africa)
Number of fishes .	9	12	8	2	9
Standard lengths .	115.0-130.2	67.5-85.5 (136.0)*	110.0-125.0 (265.0)†	105.5-122.0	117.5-166.0
In % of S.L.					
Body depth .	15.2-16.8	14.2-16.7 (19.2)	17.4-21.2	18.9-19.4	17.4-19.4
Head length .	26.2-27.5	24.2-29.2	25.2-27.0	25.4-25.7	24.2-28.2
Snout length .	7.2-8.4	(6.9) 7.5-8.8	7.2-8.2	7.0-7.6	7.4-8.4 (9.4)
Eye diameter .	7.0-7.8	(7.5) 8.9-9.8	7.0-8.6	8.3	7.8-9.0
Post-orbital distance .	8.9-9.8	8.3-9.6	9.2-10.6	8.4-8.6	8.4-9.1
Maxilla length .	8.9-9.4	9.5-9.7	8.9-9.7	—	8.7-9.2
Pectoral length .	14.8-15.1	14.9-16.0	14.7-16.2	—	15.6-17.4
Pelvic length .	8.9-9.7	8.8-9.4	7.6-8.2	—	8.2-10.2
Pre-dorsal distance .	44.2-45.5	44.0-48.0	47.0-48.4 (50.0)†	46.4	45.0-47.9 (49.4)
Pre-pelvic distance .	62.3-64.0	62.0-68.4	66.1-69.5	66.5	66.2-68.5 (70.0)
Pre-anal distance .	82.0-84.0	82.9-88.8	85.4-86.0	85.5	83.0-87.0
Gillrakers .	34-36	32-36	27-33	29-32	30-33 (36)
Dorsal rays .	iv 16-17	iii-iv 16-18	iv 15-17	iv 17-18	iii-iv 14-15
Pectoral rays .	i 14-15	i 14-16	i 14-15	i 15-16	i 14-15
Anal rays .	iii 7-8	iii 7-8	iii 8	iii 8	iii 7-8

* Single measurements outside normal range placed in parentheses.

† Type of *Perkinsia othomops*.

TABLE III.—*Proportional Measurements, Expressed as Percentages of Standard Length for Specimens of Spratelloides delicatulus from Australia (S. d. robustus) compared with Specimens from the Indo-Malayan Archipelago and the Seychelles (S. d. delicatulus)*

	Australia <i>S. d. robustus</i>	Other areas <i>S. d. delicatulus</i>
Number of specimens	10	13
Standard lengths	50.3–71.0	39.0–52.0
In % of S.L.		
Body depth	18.2–21.0	(16.7)* 17.9–20.5
Head length	25.2–28.2	24.0–26.7
Snout	7.2–7.7	6.6–7.4
Eye diameter	6.5–7.7	6.5–7.7
Post-orbital distance	9.3–10.3	8.8–10.1
Maxilla length	9.2–9.6	8.4–9.5
Pectoral length	14.2–15.8	(11.9) 14.0–15.0
Pelvic length	11.1–12.8	9.2–11.5
Pre-dorsal distance	46.3–48.0 (49.1)*	46.5–47.1 (49.2)
Pre-pelvic distance	(50.5) 53.0–57.5	53.2–56.0
Pre-anal distance	76.2–83.5	(75.0) 79.2–82.0
Dorsal rays	ii 10–11	ii 9–11
Pectoral rays	i 11–12	i 10–12
Anal rays	ii–iii 7–9	ii–iii 7–9

* Single measurements outside normal range placed in parentheses.



THE POLYCHAETE FAUNA OF
SOUTH AFRICA
PART 8: NEW SPECIES AND
RECORDS FROM GRAB SAMPLES
AND DREDGINGS

J. H. DAY



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GRAB SAMPLES AND DREDGINGS

BY

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PART 8: NEW SPECIES AND RECORDS FROM GRAB SAMPLES AND DREDGINGS

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SYNOPSIS

Recent marine collections by the University of Cape Town have revealed 27 new species of Polychaeta and 32 new records for South Africa. These are described. A new family is erected for the genus *Cossura* and three new genera are defined. The family Paraonidae is revised and a key to 17 species is drawn up.

INTRODUCTION

THE marine fauna of South Africa is at present being surveyed along a number of transect lines extending from the coast out to the edge of the continental shelf. Seven lines have been worked between Lamberts Bay on the Atlantic Coast and East London on the Indian Ocean side. An analysis of earlier polychaete samples has been presented in two reports (Day, 1960 and 1961). New species and new records for South Africa obtained from later samples are described below.

An analysis of grab samples has shown that the Polychaeta are the dominant group of benthonic animals on soft bottoms around the Cape both as regards numbers of species and numbers of individuals. Surprisingly enough there is no indication that the number of species decrease down to 200 metres; rather the reverse since there are indications that polychaetes become more numerous as the substratum changes from sand to soft mud with increasing depth. Even at a depth of 1,250 metres a 0.1 metre square van Veen grab brought up 17 species. Of course most of these species are small, many of them less than 20 mm. in length and some as small as 4 mm. These escape when a dredge is drawn up from deep water and can only be obtained by grab samples which are carefully washed through a fine sieve of 1 mm. mesh. The Polychaeta obtained by earlier dredgings around the Cape contained 171 errant species and 166 sedentary ones. The new grab samples contain representatives of many of these and in addition 32 new records for the area and 27 new species.

No attempt will be made here to list new locality records of well known species since these and earlier records will shortly be summarised in a monograph. Only

the new species and those which show major extensions of range are described. Among them are two new genera of the family Syllidae and one new genus of the family Nereidae. The discovery of five species of the family Paraonidae, in addition to the seven already reported, has provided an opportunity for revising the genera of this family and a key covering 17 species is given. In addition a new family is erected to contain the genus *Cossura* which differs widely from other genera of the family Cirratulidae.

The material upon which the present report is based was obtained with the help of funds from the South African Council of Scientific and Industrial Research to which I am very much indebted. Further, the Ernest Oppenheimer Memorial Trust made a generous grant which allowed me to work at the British Museum (Natural History) for the best part of a year. In this way I was able to compare South African material with the types or at least with identified specimens from the type locality. As a result certain types have been redescribed, several erroneous records have been removed from the South African list and many doubtful records have been confirmed.

I wish to thank my many friends at the British Museum (Natural History) for their help and courtesy during my visit, particularly Dr. F. Fraser, the Keeper of Zoology and Mr. R. Sims of the Annelid Section.

The types of all new species will be deposited in the British Museum (Natural History).

STATION LISTS

Collection data are given in the station lists below. In the systematic section the collection data for each species are given in a summarised form. Thus the records for the first species *Harmothoe antilopis* are shown as SCD 207 (1), 237 (1). This means that one specimen was found at station SCD 207 and one at station SCD 237. Reference to the station lists shows that SCD stands for south coast dredging and that station 207 was made on 30.11.60 at 34° 51' S/23° 41' E in 183 metres on a bottom of khaki coloured sand. Full details of other records can be obtained in the same way.

DREDGE AND VAN VEEN GRAB STATIONS OFF THE WEST COAST OF THE CAPE PROVINCE— SYMBOL WCD

Station No.	Date	Position	Depth (metres)	Bottom
WCD 41 .	2.5.60 .	33° 06' 5" S./17° 56' 7" E.	18-33 .	R.
WCD 53 .	15.7.60 .	34° 11' S./18° 13' E.	148 .	kh. S. M.
WCD 60 .	21.9.60 .	32° 04' 7" S./18° 12' E.	96 .	gn. M.
WCD 61 .	21.9.60 .	32° 05' S./18° 06' E.	108 .	gn. M.
WCD 63 .	21.9.60 .	32° 05' S./18° 06' E.	108 .	gn. M.
WCD 64 .	21.9.60 .	32° 05' S./17° 56' E.	128 .	gn. M.
WCD 65 .	21.9.60 .	32° 05' S./17° 56' E.	128 .	gn. M.
WCD 66 .	21.9.60 .	32° 05' S./18° 14' E.	83 .	?
WCD 67 .	22.9.60 .	32° 44' S./18° 01' E.	11 .	bl. M.
WCD 73 .	8.10.60 .	34° 25' S./17° 36' E.	1240 .	kh. M.
WCD 79 .	8.10.60 .	34° 17' S./17° 53' E.	320 .	gn. S. M.

Station No.	Date	Position	Depth (metres)	Bottom
WCD 82	21.9.60	32° 05' S./17° 56' E.	128	gn. M.
WCD 83	8.10.60	34° 17' S./17° 53' E.	320	gn. S. M.
WCD 85	3.7.61	33° 06.4' S./17° 44.9' E.	146	gn. bl. M.
WCD 86	3.7.61	33° 06.4' S./17° 44.9' E.	146	gn. bl. M.
WCD 87	3.7.61	33° 06.2' S./17° 49' E.	88	d. gn. M. R.
WCD 90	2.7.61	32° 05' S./18° 16.7' E.	39	co. wh. S. & Sh.
WCD 91	2.7.61	32° 05.5' S./18° 17.3' E.	27	co. wh. S. & Sh.
WCD 92	2.7.61	32° 05' S./18° 16.7' E.	39	co. wh. S. & Sh.
WCD 94	2.7.61	32° 05.3' S./18° 15.8' E.	54	S.
WCD 97	3.7.61	33° 04.2' S./17° 49' E.	88	d. gn. M. & R.
WCD 103	2.7.61	32° 05.3' S./18° 15.8' E.	54	kh. M.
WCD 106	3.7.61	33° 06.5' S./17° 32.9' E.	183	d. gn. M.
WCD 108	2.7.61	32° 08' S./17° 39' E.	172	f.d. gn. M.
WCD 109	2.7.61	32° 08' S./17° 39' E.	172	f. d. gn. M.
WCD 110	2.7.61	32° 08' S./17° 39' E.	172	f. d. gn. M.
WCD 112	3.7.61	33° 06.4' S./17° 47.2' E.	141	d. gn. M.
WCD 115	3.7.61	33° 06.5' S./17° 32.9' E.	183	d. gn. M.
WCD 116	3.7.61	33° 06.5' S./17° 32.9' E.	183	d. gn. M.
WCD 118	3.7.61	33° 06.4' S./17° 44.9' E.	146	gn. bl. M.
WCD 121	2.7.61	32° 08' S./17° 39' E.	172	f. d. gn. M.
WCD 122	2.7.61	32° 08' S./17° 39' E.	172	f. d. gn. M.

DREDGE AND VAN VEEN GRAB STATIONS IN FALSE BAY—SYMBOL FAL

Station No.	Date	Position	Depth (metres)	Bottom
FAL 284	23.9.54	Roman Rock (diving)	12-14	S. Sh.
FAL 342	31.1.59	34° 11' S./18° 35.5' E.	44	f. br. S.
FAL 375	25.2.59	34° 16.8' S./18° 42.8' E.	60	gn. S. Sh.
FAL 390	15.11.60	34° 12.6' S./18° 29.1' E.	40	kh. M.
FAL 397	15.5.61	34° 12.5' S./18° 37' E.	48	kh. S. & Sh.
FAL 406	16.5.61	34° 08.8' S./18° 33.5' E.	31	f. kh. S.
FAL 413	15.5.61	34° 12.5' S./18° 37' E.	48	kh. S. & Sh.
FAL 419	15.5.61	34° 12.5' S./18° 37' E.	48	kh. S. & Sh.
FAL 422	15.5.61	34° 12.5' S./18° 37' E.	48	kh. S. & Sh.
FAL 424	15.5.61	34° 12.5' S./18° 37' E.	48	kh. S. & Sh.

DREDGE AND VAN VEEN GRAB SAMPLES OFF THE SOUTH COAST OF THE CAPE PROVINCE—
SYMBOL SCD

Station No.	Date	Position	Depth (metres)	Bottom
SCD 130	3.6.60	34° 48' S./22° 06' E.	100	co. kh. S.
SCD 136	28.8.60	34° 35' S./21° 56' E.	78	co. & f. Sh.
SCD 154	25.11.60	34° 03' S./25° 59' E.	84	R.
SCD 156	25.11.60	34° 03' S./25° 59' E.	84	R.
SCD 170	24.11.60	33° 58.9' S./25° 41.4' E.	4-11	R.
SCD 182	30.11.60	34° 20' S./23° 31' E.	110	R. kh. S.
SCD 185	25.11.60	34° 13' S./26° 04' E.	124	gr. gn. S.
SCD 187	30.11.60	34° 10' S./23° 32' E.	97	gn. M.
SCD 193	29.11.60	34° 04.3' S./23° 25.8' E.	45	gn. M.
SCD 197	29.11.60	34° 07.5' S./23° 31.7' E.	79	f.S.
SCD 200	30.11.60	34° 10' S./23° 32' E.	97	gn. M.
SCD 207	30.11.60	34° 51' S./23° 41' E.	183	kh. S.
SCD 212	24.11.60	33° 58.8' S./25° 42.2' E.	26	co. S. br. Sh.

SCD 214	.	25.11.60	.	34° 03' S./25° 58' E.	.	78	.	co. gr. S. br. Sh.
SCD 215	.	25.11.60	.	34° 03' S./25° 58' E.	.	78	.	co. gr. S. br. Sh.
SCD 218	.	25.11.60	.	34° 03' S./25° 58' E.	.	78	.	co. gr. S. br. Sh.
SCD 220	.	29.11.60	.	34° 02' S./23° 28.4' E.	.	49	.	S.M.R.
SCD 223	.	25.11.60	.	34° 13' S./26° 04' E.	.	124	.	gr. gn. S.
SCD 227	.	29.11.60	.	34° 07.5' S./23° 31.7' E.	.	79	.	f. S.
SCD 228	.	5.12.60	.	35° 43.5' S./20° 31' E.	.	143	.	gn. M.
SCD 232	.	4.12.60	.	36° 28.5' S./21° 11' E.	.	183	.	kh. S.
SCD 233	.	4.12.60	.	36° 28.5' S./21° 11' E.	.	183	.	kh. S.
SCD 236	.	30.11.60	.	34° 51' S./23° 41' E.	.	183	.	kh. S.
SCD 237	.	30.11.60	.	34° 51' S./23° 41' E.	.	183	.	kh. S.
SCD 245	.	29.11.60	.	34° 02' S./23° 28.4' E.	.	49	.	S. M. R.
SCD 246	.	29.11.60	.	34° 02' S./23° 28.4' E.	.	49	.	S. M. R.
SCD 247	.	29.11.60	.	34° 04.3' S./23° 25.8' E.	.	45	.	gn. M.
SCD 251	.	30.11.60	.	34° 48' S./23° 39' E.	.	148	.	R.
SCD 275	.	30.11.60	.	34° 51' S./23° 41' E.	.	183	.	kh. S.
SCD 284	.	6.2.62	.	33° 01' S./27° 55' E.	.	7	.	f. wh. S.
SCD 288	.	6.2.62	.	33° 04' S./27° 57' E.	.	84	.	co. S. Sh.
SCD 298	.	6.2.62	.	33° 09' S./28° 02' E.	.	84	.	?

SYSTEMATIC ACCOUNT

Family **APHRODITIDAE**Sub-family **POLYNOINAE***Harmothoe antilopis* McIntosh, 1876

(Text-fig. 1a-f)

Harmothoe antilopis McIntosh, 1876: 383, pl. 69, figs. 4-6; McIntosh, 1900: 334, pl. 28, fig. 13; pl. 32, fig. 16; pl. 38, figs. 24-25; Fauvel, 1923: 56, fig. 19 a-l.

RECORDS. SCD 207 (1), 237 (1).

NOTES. These South African specimens have been checked as identical with the types in the British Museum (Natural History) (No. 1921-5-1-437-438) obtained in 358-567 fathoms off Scotland by the "Porcupine".

The resemblance is in fact even closer than the published descriptions of the types would suggest. The type material consists of two broken specimens each about 20 mm. long. The prostomium (Text-fig. 1a) is roughly square, not tapered anteriorly, the anterior pair of eyes is large and their position is characteristic for they are directly below the small but well marked prostomial peaks. The median antenna is missing both from the types and the South African specimens but the laterals are present; they are small, tapered and, like the dorsal cirri, have numerous long papillae. The elytra (Text-fig. 1b) are oval with fringed margins and numerous chitinous tubercles (Text-fig. 1c) which are best described as tall crowns for they are cylindrical with 4-5 divergent projections at the truncate end. In the South African specimens (but not in the types) some of the tubercles near the posterior margin are twice the size of the rest and instead of blunt projections each has three saucer-like depressions the edges of which form prominent flanges (see Text-fig. 1c').

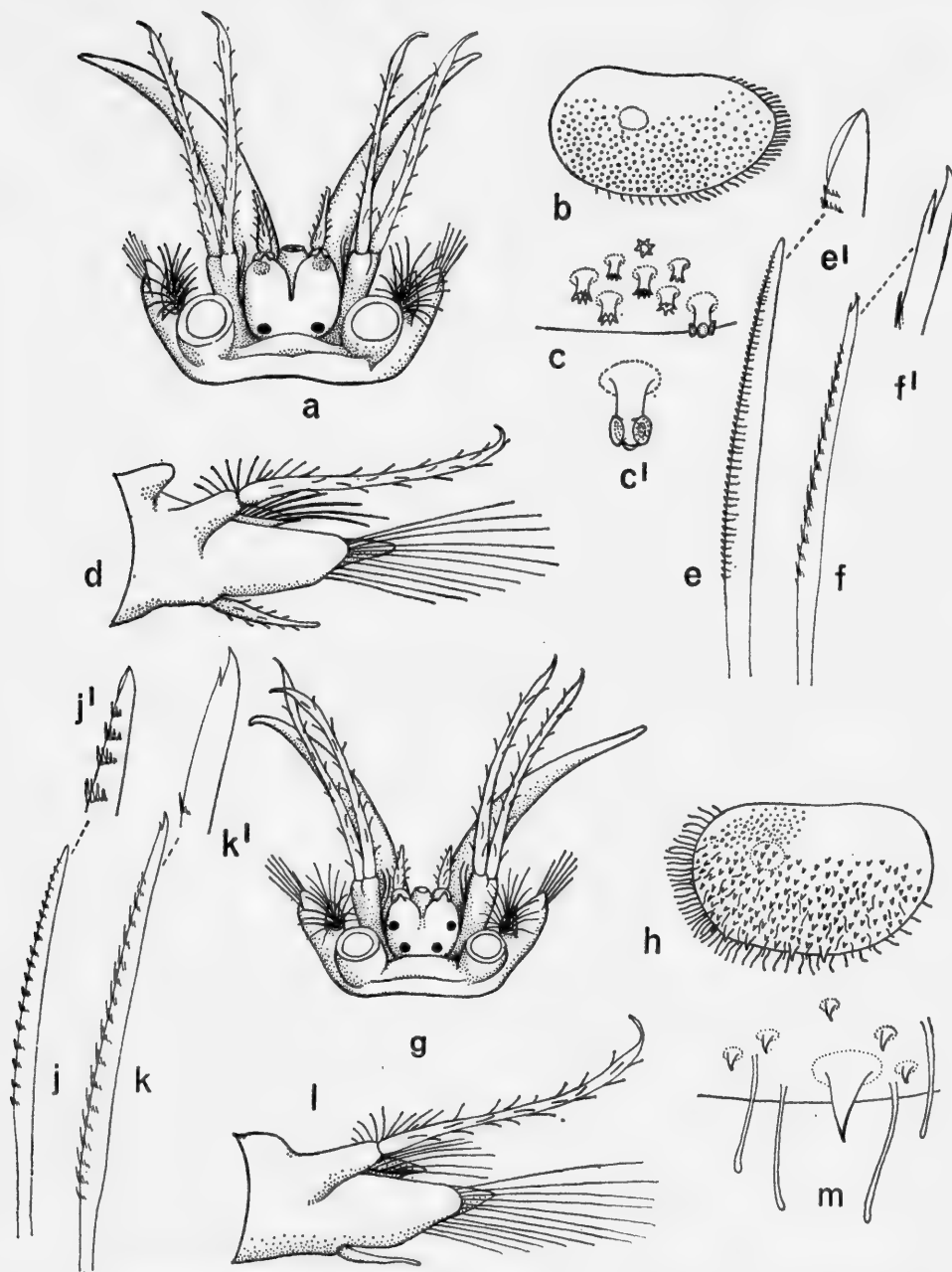


FIG. 1. *Harmothoe antilopis* : (a) head ; (b) elytron ; (c, c') details of elytrous tubercles near posterior margin ; (d) posterior view of parapodium ; (e, e') notoseta and details of tip ; (f, f') neuroseta and details of tip. *Harmothoe lagiscoides serrata* : (g) head ; (h) elytron ; (j, j') notoseta and details of tip ; (k, k') neuroseta and details of tip ; (l) posterior view of parapodium ; (m) details of elytrous tubercles near posterior margin.

The dorsal cirri (Text-fig. 1 *d*) are tapered and just shorter than the neurosetae. The notopodium is well developed and the neuropodium has a triangular presetal lip. The notosetae (Text-fig. 1 *e*) are much more closely serrated than the figures of McIntosh and Fauvel would suggest; the tips (Text-fig. 1 *e'*) are blunt and in the South African forms they are flanged. The neurosetae (Text-fig. 1 *f*) have about 15 rows of spinules and long naked and bidentate tips (Text-fig. 1 *f'*) with the secondary tooth half the length of the terminal one.

The two most characteristic features are the position of the eyes and the tall crowns on the elytra. Both *Harmothoe aquiseta* and *Antinoe epitoca* have the first pair of eyes antero-ventral in position but there are obvious differences in the elytra and setae.

H. antilopis seems to be a deep water species. It has long been known from the Atlantic coasts of Europe but when more samples have been obtained at the edge of the continental shelf its distribution may prove to be much wider than is known at present.

***Harmothoe lagiscoides serrata* subsp. n. (Text-fig. 1 *g-m*)**

RECORDS. WCD 112 (1).

DIAGNOSIS. Differs from *H. lagiscoides* (Wiley, 1902) in having strongly serrated notosetae, neurosetae with long knife-bladed tips and only a single row of giant curved spines on the posterior margin of the elytra.

DESCRIPTION. The type locality is 33° 06.4' S/17° 47.2' E in 141 metres. The single specimen is an ovigerous female broken into four pieces, but if complete it would measure about 20 mm. The body is well tapered and creamy brown in alcohol.

The prostomium (Text-fig. 1 *g*) has well marked frontal peaks. The eyes are well developed and the anterior pair are about half-way back on the sides of the prostomium. The median antenna is missing but the laterals are present. They are obviously ventral in origin with stout ceratophores and small tapered papillose ceratostyles two-thirds the length of the prostomium. The palps and tentacular cirri are long and tapered and the latter are beset with long slender papillae.

The dorsal cirri (Text-fig. 1 *l*) are similar to the tentacular cirri and exceed the neurosetae in length. Anterior elytra are missing but those in the middle of the body are large, delicate and faintly reniform in shape (see Text-fig. 1 *h*). The lateral and posterior margins (Text-fig. 1 *m*) bear fringes of very long slender papillae with faintly knobbed tips. Similar papillae are scattered over the elytron surface but are difficult to see since the elytron is mottled with pale brown and bears numerous well marked chitinous tubercles. The tubercles near the anterior margin are minute and hemispherical but the great majority are stout thorns with faintly curved tips. They are scattered over the rest of the elytron and are uniform in size except for 4-5 in a row along the posterior margin which are much larger than the others.

The notopodia are normally developed and bear numerous notosetae. The neuropodia (Text-fig. 1 *l*) have pointed presetal lobes and shorter, more triangular post-

setal lips. The ventral cirri are very small, markedly tapered and do not extend to the base of the neurosetae. Nephridial papillae are well developed from setiger 5 onwards.

Notosetae vary in length and are slightly stouter than the neurosetae. An average notoseta (Text-fig. 1 j) has numerous strongly developed rows of serrations extending over more than half its length and the tip (Text-fig. 1 j') is pointed and faintly flanged. The neurosetae also vary in length and development of the secondary tooth. An average neuroseta from the middle of the series (Text-fig. 1 k) has over 20 rows of long spinules and a long blade-like naked tip (Text-fig. 1 k') with a small secondary tooth. As usual, superior neurosetae are finer with a better marked secondary tooth and inferior ones are shorter and stouter with a finer secondary tooth.

Wiley (1902) described *Harmothoe spinosa* var. *lagiscoides* from Antarctica. Bergström (1916) raised *H. lagiscoides* to species rank and Hartman (1953) agreed. According to Bergström the development of giant spines on the elytra is variable but Bergström, Hartman and Monro (1936) all agree that the notosetae are either smooth or only faintly serrated. It is in this character particularly that the South African form differs from the Antarctic species. Holotype: B.M.(N.H.), Reg. No. 1963.1.2.

Antinoe epitoca Monro, 1930

Antinoe epitoca Monro, 1930: 67, fig. 19 a-f.

RECORDS. FAL 406 (1).

NOTES. As far as I am aware this species has not been recorded since Monro's original description of the type from dredgings off Angola. The present record extends its range to False Bay. Monro's specimen lacked elytra but these are present on the Cape specimens and are large and oval with smooth surfaces and entire margins.

A. epitoca is easily distinguished from *A. lactea* Day by the position of the eyes under the prostomial peaks and the very much fainter serrations on the notosetae.

Subfamily SIGALIONINAE

Pholoe dorsipapillata Marenzeller, 1893

Pholoe dorsipapillata Marenzeller, 1893: 30; Fauvel, 1923, fig. 23 n-q.

RECORDS. SCD 298 (1).

NOTES. The single specimen is well preserved and permits me to modify Fauvel's description.

This species is broader and tougher than *P. minuta* and the elytra are very hard, almost brittle with successive layers of chitin forming marked concentric rings on the elytra. The median antenna arises from a short ceratophore and there is a papillose subterminal swelling preceding the filiform tip. It is usually stated that in all species of *Pholoe* there are no lateral antennae, but in this specimen there are

indications that minute lateral antennae are present fused to the dorsal surface of the bases of the tentacular cirri. Other points of difference from *P. minuta* are that *P. dorsipapillata* has a single tentacular cirrus, not two, and that there are numerous fine setae at the base. The neuropodium moreover has a long papilla at its apex and the shaft-heads of the neurosetae are more finely serrated than those of *P. minuta*.

Family PISIONIDAE

Pisione africana sp. n.

(Text-fig. 2 *a-e*)

RECORDS. SCD 136 (1 juv.); 170 (1-type); 212 (6 juvs.). FAL 419 (2 juvs.); 424 (2 juvs.).

DESCRIPTION. All specimens except one are juveniles 2–5 mm. long. The single adult from station SCD 170, dredged at 33° 58.9' S./25° 41.4' E. is designated the holotype. It is 15 mm. long with 75 segments and is uniformly pale in alcohol.

The prostomium (Text-fig. 2 *a*) is small, indistinct and almost completely fused to the enveloping peristome. A pair of cephalic eyes probably formed by the fusion of two pairs is visible through the skin at the level of setiger 1. The two pairs of jaws when dissected proved to be curved and pointed with flanged bases but have no teeth. The large cirriform palps arise from basal sheaths fused to the peristome. The latter is very large and extends forward completely embracing the prostomium and bears two pairs of tentacular cirri above the bases of the palps. The superior pair is long and tapered, simulating antennae, but the inferior pair is small and papilliform. Both pairs are essentially similar in structure to the cirri of setiger 1 and differ from the palps. The peristomial segment also has a pair of very large acicula whose expanded ends project through the skin in front of the mouth and probably assist in feeding. Their posterior ends diverge outwards and almost reach the bases of the first pair of parapodia. The first setigerous segment is relatively short and not very distinct from the peristomium. The parapodium consists of a papilliform dorsal cirrus similar to those of later segments, a conical setigerous lobe and a long tapering ventral cirrus which is directed forwards and just reaches the bases of the palps. Setiger 2 is essentially similar except that in the adult type specimen the dorsal cirrus is markedly larger than that of the first or third setiger. In juveniles this is not obvious. Later parapodia (Text-fig. 2 *e*) are uniform in structure. Each has a flask-shaped dorsal and ventral cirrus which is indistinctly jointed near the ciliated tip and a long setigerous lobe with small presetal and post-setal lips. No genital papillae were seen.

Each parapodium has two pale internal acicula and about 5 setae. The superior one (Text-fig. 2 *b*) is simple and stouter than the rest with an expanded, obliquely truncate end, sometimes incised to form indistinct teeth. The other setae are all compound. One is rather slender (Text-fig. 2 *c*) with a tapering sword-like blade and the other three (Text-fig. 2 *d*) have short, straight falcigerous blades.

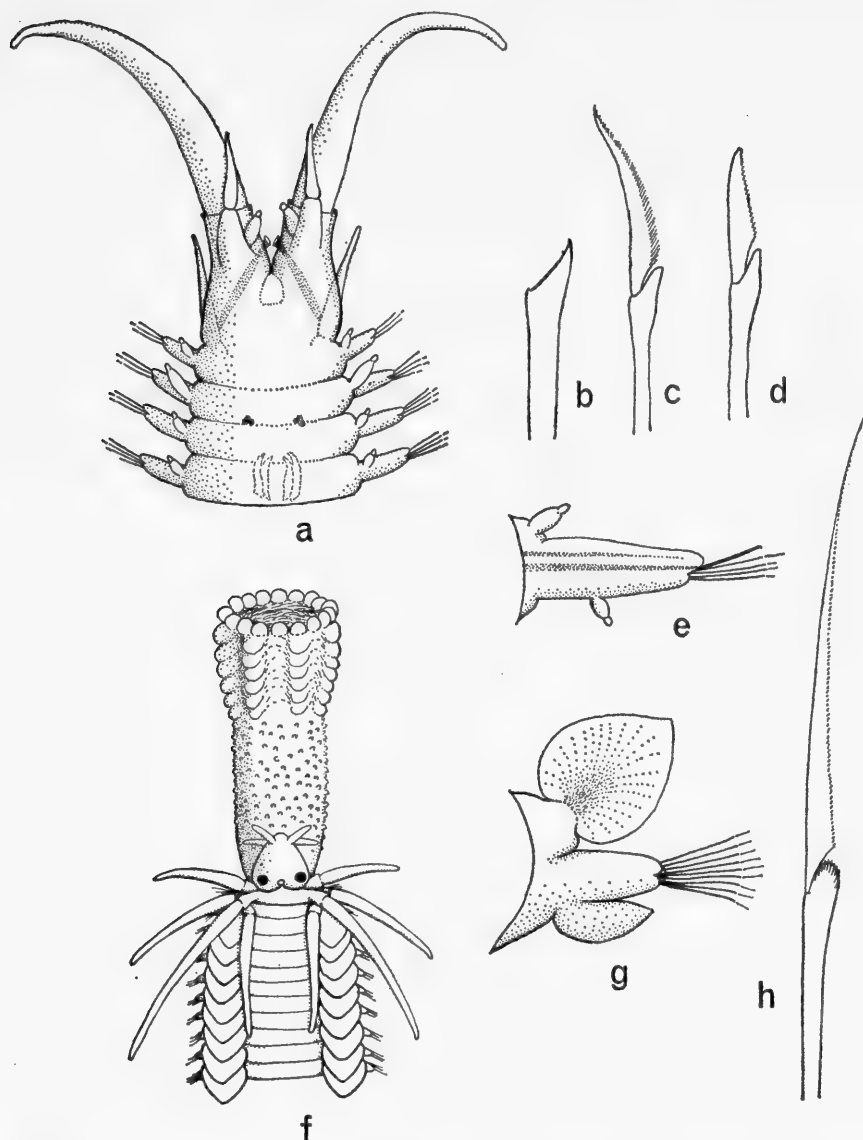


FIG. 2. *Pisione africana*: (a) anterior end; (b) superior simple seta; (c) superior compound seta; (d) inferior compound seta; (e) parapodium. *Phyllodoce schmardaei*: (f) anterior end; (g) parapodium; (h) seta.

Pisione is a rare genus and Hartman (1959) listed only 6 species. *P. africana* differs from *P. remota* (Southern, 1914) in the character of the setae and the possession of an enlarged dorsal cirrus on setiger 2. In this it is closer to *P. oerstedii* Grube 1857 from Peru as redescribed by Ehlers (1901) but again the setae differ. In particular the possession of a compound seta with a long sword-like blade is characteristic.

There has been much discussion as to the homology of the large cirriform appendages with sheathed bases at the front of the head. Southern (1914) suggested that they are palps which have become attached to the large, forwardly produced peristome. This interpretation which is accepted here makes them homologous to the palps of *Pisionidens indica*. In the latter the prostomium is well developed and anterior to the peristome. It bears a pair of antennae and a pair of palps which also have sheathed bases. The peristome bears two normal pairs of tentacular cirri. In *Pisione* the tentacular cirri are dorsal to the palps and the inferior pair are greatly reduced. Holotype: B.M.(N.H.), Reg. No. 1963.1.12.

Family PHYLLODOCIDAE

Phyllodoce schmardaei sp. n.

(Text-fig. 2 f-h)

Phyllodoce macrophthalma (non *Phyllodoce macrophthalma* Grube, 1857: 169.)? Schmarda, 1861: 84, pl. 30, fig. 234;? Ehlers, 1913: 454;? Day, 1960: 297.

RECORDS. FAL 422 (1).

DESCRIPTION. Hartman (1959) showed that the name *Phyllodoce macrophthalma* was first used by Grube 1856 and that Schmarda's name is a homonym. There is also some doubt as to whether the specimen described by Schmarda "in Atlantischen Meer" is identical to those from France described by Saint Joseph (1888), Fauvel (1923) and Day (1960). For these reasons the South African species is given a new name and described briefly below.

The holotype dredged in False Bay at station FAL 422 is 30 mm. long with 60 segments and when fresh it was uniformly green in colour.

The prostomium (Text-fig. 2 f) is cordate with rather long frontal antennae, a pair of large eyes and a small occipital papilla. The basal half of the proboscis is lightly papillose and the distal half has 6 rugose ridges. The first tentacular segment is fused to the prostomium and not visible dorsally, but the second and third are distinct and separate. All tentacular cirri are cylindrical and fairly long. Setae are present on tentacular segments 2 and 3 giving the formula $1 + S_{\frac{1}{2}} + S_{\frac{1}{N}}$. Anterior dorsal cirri (Text-fig. 2 g) are cordate and about as broad as long but become distinctly longer than broad posteriorly. The setigerous lobe is blunt apically with subequal and rounded presetal lips. The ventral cirrus is oval with a pointed tip rather shorter than the setigerous lobe. The setae (Text-fig. 2 h) have oval shaft-heads which are denticulate distally and blades of normal length. Holotype: B.M.(N.H.), Reg. No. 1963.1.13.

Phyllodoce tubicola sp. n.

(Text-fig. 3 a-c)

RECORDS. SCD 200 (1), 232 (1); FAL 397 (1).

DESCRIPTION. The holotype is from station SCD 200 dredged on the Agulhas

Bank at $34^{\circ} 10' S / 23^{\circ} 32' E$. in 97 metres. It is encased in a delicate and transparent tube which is closely ringed. The body is brownish in alcohol without any obvious pattern. It is 30 mm. long and very slender with about 80 segments.

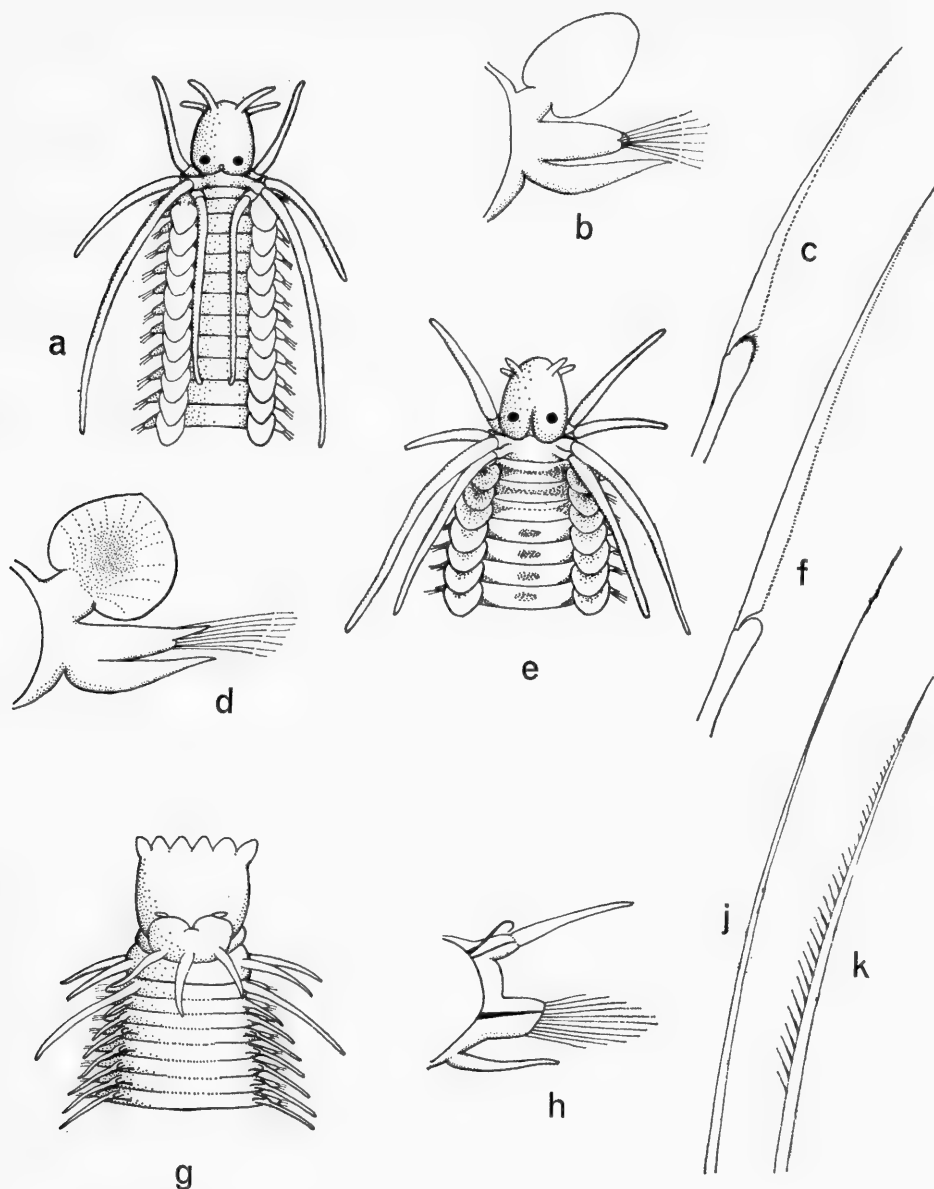


FIG. 3. *Phyllodoce tubicola* : (a) anterior end ; (b) parapodium ; (c) seta. *Phyllodoce longipes* : (d) parapodium ; (e) anterior end ; (f) seta. *Ancistrostylis parva* : (g) anterior end ; (h) parapodium ; (j) long central neuroseta ; (k) short outer neuroseta.

The prostomium (Text-fig. 3 *a*) is oval and longer than broad with a small posterior occipital notch and a minute occipital papilla. The frontal antennae are rather long but the eyes are not enlarged. The proboscis on dissection proved to have small irregular papillae on the basal part, a brown band near the middle and then six rugose ridges distally.

The first tentacular segment is fused to the prostomium and not visible dorsally but the second and third are distinct and separate. The tentacular cirri are all rounded in section and very long, the longest being D_2 which reaches back to setiger 8. Setae are present only on the third tentacular segment, the formula thus being $1 + O_{\frac{1}{2}} + S_N^1$.

The dorsal cirri (Text-fig. 3 *b*) are oval to cordate anteriorly but become longer, almost hastate posteriorly. The setigerous lobe is bluntly rounded distally with a notched presetal lip. The ventral cirrus is pointed and obviously longer than the setigerous lobe. Each parapodium bears about 12 setae with oval, striated shaft-heads and long tapering blades (see Text-fig. 3 *c*).

The only other South African species with setae restricted to the third tentacular segment is *P. (Anaites) capensis*, but here the prostomium is partly covered by the fused first and second tentacular segments. Several European species listed by Fauvel, 1923 have the same tentacular formula but differ either in the shape of the prostomium or the character of the proboscis. The genus *Phyllodoce* does not normally live in a tube and it is suspected that the delicate tube in which the holotype (but not the paratypes) was encased may have been a temporary mucous secretion which hardened around the worm during preservation. Holotype: B.M.(N.H.), Reg. No. 1963.1.14.

Phyllodoce (Anaitides) longipes Kinberg, 1865

(Text-fig. 3 *d-f*)

Phyllodoce longipes Kinberg, 1865: 241; Ehlers, 1901: 72, pl. 7, figs. 1-4. (non *Phyllodoce longipes*: Monro, 1930: 73, fig. 21; nec Monro, 1936: 101)

RECORDS. FAL 342 (3).

DESCRIPTION. The largest specimen is 25 mm. long but the last few segments are missing. The anterior end is shown in Text-fig. 3 *e*. The first three segments following those that bear tentacular cirri are dusky, the later ones have three rows of blurred spots. The prostomium is longer than broad with a small posterior notch but no occipital papilla. The proximal half of proboscis has 6 long regular rows of papillae at the sides, and about 14 papillae per row. The distal half has 6 rugose ridges. The first tentacular segment is fused to the prostomium and is not visible dorsally; the second segment is indistinct, but the third segment is distinct and separate. Tentacular cirri are all tapered and rounded in section, the longest being D_2 which is very long. No setae are present on any tentacular segment the formula being $1 + O_{\frac{1}{2}} + O_{\frac{1}{N}}$. The dorsal cirri (Text-fig. 3 *d*) are large and cordate anteriorly but become broader, almost reniform posteriorly. They are dusky, often with a central darker spot. The setigerous lobe has the superior

division of the presetal lip long and pointed and the ventral cirrus has a pointed tip as long as the setigerous lobe. The setae (Text-fig. 3 *f*) have oval striated shaft-heads and serrated tapering blades.

These South African specimens agree very well with Ehlers' description and figures and have the same three characteristically dusky segments following those that bear the tentacular cirri. But Ehlers' account of the tentacular segments is confused and in the text he makes no mention of the fact that the first two segments are fused to the prostomium. Bergstrom (1914, p. 149), who examined Kinberg's type from Valparaiso found it in a poor condition and does not discuss the point, but his text-figure 47 is an excellent illustration of the characteristic parapodium.

Monro's specimens were examined in the British Museum and, as he stated, they have setae in the second and third tentacular segments. The coloration is also different and they obviously belong to a different species. Incidentally there is no aciculum in the dorsal cirrophore.

Family PILARGIDAE

Ancistroyllis parva sp. n.

(Text-fig. 3 *g-k*)

RECORDS. FAL 390 (2); SCD 200 (2).

DESCRIPTION. The holotype is the largest specimen from station SCD 200 dredged at 34° 10' S./23° 32' E. in 97 metres. It measures 10 mm. by 0.7 mm. for 60 segments. The body is rather flattened, tapered posteriorly, and pale in alcohol. There is no narrowed neck region.

The prostomium (Text-fig. 3 *g*) is broader than long without any posterior indentation. A pair of palps with broad flattened palpophores and small palpostyles arise from the anterior margin with a notch between them. There are three tapered antennae each equal to half the width of the peristome but there are no eyes. The proboscis is everted and muscular with 12 marginal papillae; the 8 dorsal ones are stout and conical but the 4 ventral ones are smaller. The peristome bears 2 pairs of tentacular cirri which are the same length as the antennae. The first setiger has a dorsal cirrus which is even longer than the tentacular cirri, a normal setigerous lobe and a ventral cirrus. The second setiger has a rather short dorsal cirrus and a normal setigerous lobe but no ventral cirrus. Subsequent parapodia (Text-fig. 3 *h*) are all essentially similar. The dorsal cirri are smoothly tapered and there is a vague joint between the cirrus and its short stout cirrophore. The setigerous lobe is bluntly truncate and the ventral cirrus is similar to the dorsal one but smaller.

There are no notosetae on the first three setigers. From the fourth onwards a smooth, stout recurved hook arises from the dorsal cirrophore which is thus homologous to a vestigial notopodium. The neurosetae are all simple capillaries. The short outer ones (Text-fig. 3 *k*) have long spinules along one margin but the much longer setae in the centre of the bundle (Text-fig. 3 *j*) have smooth blades.

A. parva is allied to *A. tentaculata* Treadwell 1941 from Long Island Sound, U.S.A. Both are small species with long antennae and dorsal cirri. Both lack a

ventral cirrus on setiger 2 and have notopodial hooks from setiger 4 onwards. But Treadwell figures *A. tentaculata* as having the posterior margin of the prostomium deeply excavate. In *A. parva* the posterior margin of the prostomium is smoothly curved.

Two species of *Ancistrosyllis* have previously been recorded from southern Africa. Ehlers (1908) recorded *A. robusta* from Angola. This is a much larger species with notopodial hooks appearing on setiger 69. Ehlers does not mention whether there is a ventral cirrus on setiger 2 or not. *Ancistrosyllis cf. constricta* described by me (Day, 1957, p. 71) is almost certainly a juvenile. It lacks a ventral cirrus on setiger 2 but the notopodial hooks start on setiger 8 and from setiger 3 onwards there are 1-2 fine notopodial capillaries in all feet. Holotype: B.M.(N.H.) Reg. No. 1963.1.22.

Loandalia capensis sp. n.

(Text-fig. 4 a-d)

RECORDS. SCD 220 (2).

DESCRIPTION. The holotype which was dredged at 34° 02' S./23° 28.4' E. in 49 metres consists of one specimen broken into three pieces with a total of 56 segments measuring 15 mm. The pygidium is missing. There is also a headless fragment of a smaller specimen. The body is rounded in section and about 0.8 mm. broad. The segments are about twice as broad as long though the first few segments are shorter, about 4 times as broad as long. The general appearance is that of a Maldanid for the head appendages are not obvious, the parapodia are very small and there are deep constrictions between the segments.

The head and first three setigers (Text-fig. 4 a) are covered with conical papillae but the rest of the surface is smooth.

The prostomium is small and not clearly separated from the peristomium. It bears a pair of palps with large palpophores and small palpostyles but there are no antennae nor eyes. The proboscis is partly everted and is soft and unarmed. The peristome is clearly separated from setiger 1. Like the other anterior segments it is broader than long and careful examination shows that it bears two pairs of tentacular cirri. These are not much larger than the scattered papillae but quite definite.

The parapodia are inconspicuous throughout. There is a low papilliform notopodial lobe supported by an aciculum but no dorsal cirrus. The neuropodia are a little larger and broadly conical with 2 acicula and a minute ventral cirrus just below the apex. None of the parapodia has any sign of gills.

The first 7 setigers have no notosetae, only an internal aciculum. From setiger 8 onwards each notopodium (Text-fig. 4 b) bears a single stout recurved hook (Text-fig. 4 c) which is granular near the apex. There are no capillaries. The neurosetae (Text-fig. 4 d) are 3-4 capillaries per parapodium. Each has a narrow hairlike blade which is either smooth or very faintly serrated and tapers to a slender tip.

The absence of antennae and the presence of very small tentacular cirri places this species in an intermediate position between *Loandalia* and *Pilargis*. The poorly developed parapodia suggest that it is closer to *Loandalia*.

L. capensis is the fourth recorded species of this rare genus. The other three lack tentacular cirri and *L. aberrans* Monro, 1936 which was recorded from Angola also has gills on the posterior parapodia. Holotype : B.M.(N.H.), Reg. No. 1963.1.25.

Family **HESIONIDAE**
***Oxydromus capensis* sp. n.**

(Text-fig. 4 *e-j*)

RECORDS. SCD 200 (1) ; FAL 390 (1 + 1 juv.) ; WCD 112 (1), 118 (1).

DESCRIPTION. The holotype was selected from station WCD 112 dredged off Saldanha Bay in 141 metres on dark green mud. It is 5 mm. long for 20 segments but the posterior half is missing and the complete worm was probably double this length. The body is uniformly pale in alcohol.

The prostomium (Text-fig. 4 *h*) is roughly rectangular and twice as broad as long. The three antennae all arise from the anterior margin and the median is only half the length of the laterals. The biarticulate palps are much stouter than the lateral antennae but not longer. The palpostyle is ovoid and slightly shorter than the palpophore. The prostomium bears two pairs of eyes and the anterior pair are reniform and larger than the posterior pair. The proboscis is muscular and lacks jaws but has 10 conical, widely separated papillae around its margin.

There are 8 pairs of faintly articulated tentacular cirri borne on 4 partially fused segments. The first pair of tentacular cirri are shorter than the rest which are considerably longer than the body is broad.

The first 5-7 segments are uniramous and the rest biramous. The dorsal cirri are mounted on short cirrophores and are smooth and tapered, not annulated. Apart from the first which is equal to three-quarters of the body width, the dorsal cirri are about equal to half the body width. The first few cirrophores have internal acicula but no setae ; from setiger 5 onwards a notopodial papilla appears on the ventral side of the cirrophore and by setiger 7 it obviously bears setae. Whether small notosetae are present on setigers 5 and 6 is doubtful. On later parapodia (Text-fig. 4 *j*) the notopodium is small but quite conspicuous and bears about 10 setae. The neuropodia are always well developed. Each is roughly cylindrical with numerous setae, and bears a triangular presetal lobe, a shorter rounded postsetal lip and a tapered ventral cirrus.

The notosetae include capillaries with smooth flattened blades (Text-fig. 4 *f*) and 3-4 forked setae (Text-fig. 4 *e*). The neurosetae (Text-fig. 4 *g*) are all compound and falcigerous with bidentate blades of varying length. The margin of the blade is minutely serrated and the bidentate apex is formed by a strong terminal tooth and a long slender secondary tooth.

The only record of *Oxydromus* from southern Africa is *Oxydromus* sp. Augener, 1918, p. 225 from Angola. This is incompletely known and possibly has jaws, in which case it belongs to a different genus. *O. capensis* is close to *O. arenicolus* La Greca, 1946 from the Mediterranean and to the subspecies *O. a. glabrus* Hartman, 1961 from California. All three have 10 widely spaced marginal papillae on the proboscis while other species have numerous marginal papillae. However, *O.*

capensis differs from *O. arenicolus* in that the notosetae do not appear before setiger 5 and include both forked setae and capillaries. Forked setae were also reported by Augener for the doubtful *Oxydromus* sp. from Angola. *O. arenicolus* is also said to have annulated dorsal cirri whereas those of *O. capensis* appear to be smooth. Holotype: B.M.(N.H.), Reg. No. 1963.1.28.

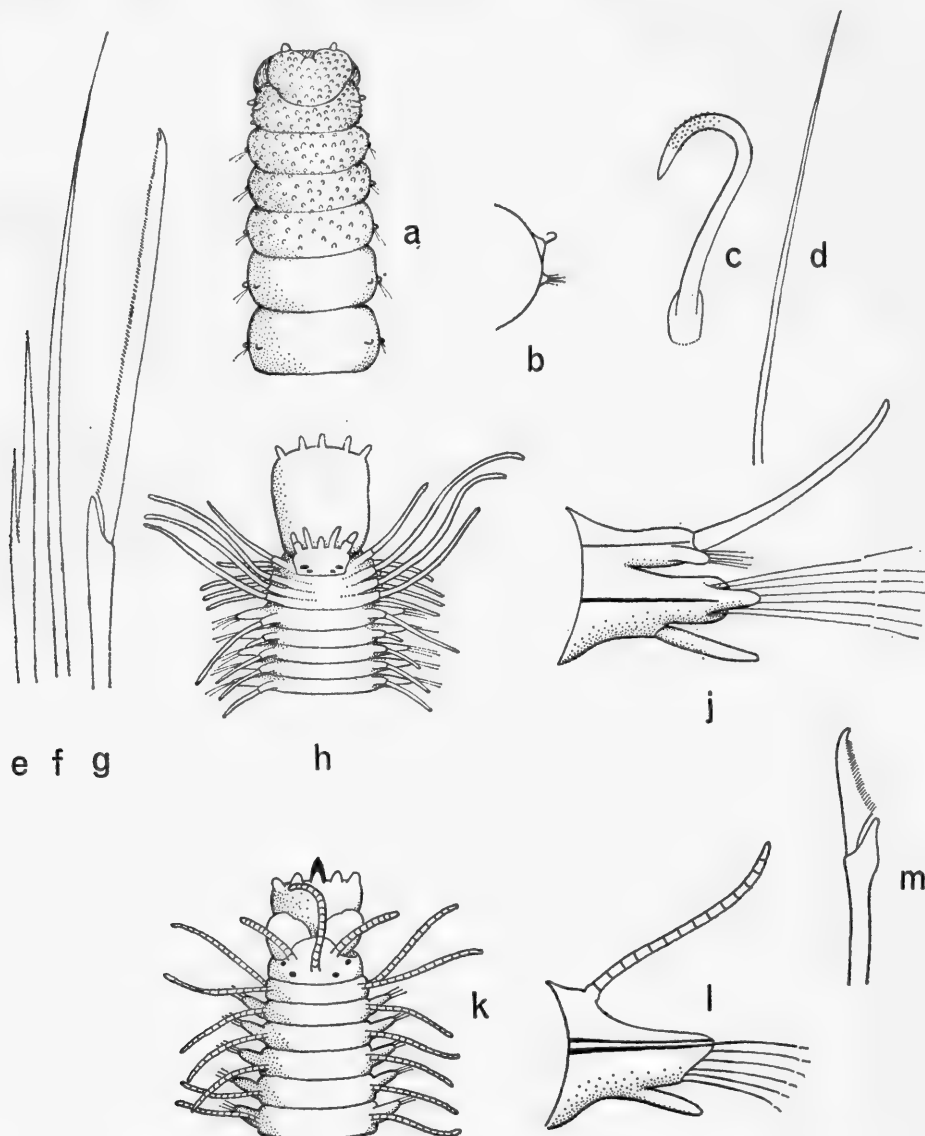


FIG. 4. *Loandalia capensis*: (a) anterior end; (b) 12th parapodium; (c) notopodial hook; (d) neuroseta. *Oxydromus capensis*: (e) notopodial forked seta; (f) notopodial capillary; (g) neuroseta; (h) anterior end; (j) anterior view of parapodium. *Syllis benguellana*: (k) anterior end; (l) parapodium; (m) seta.

Family SYLLIDAE

Syllis benguellana sp. n.(Text-fig. 4 *k-m*)

RECORDS. WCD 91 (ca. 100).

DIAGNOSIS. A threadlike species with slender dorsal cirri having about 15 long joints. Setae unidentate.

DESCRIPTION. Numerous specimens were obtained by a van Veen grab at station WCD 91 at 32° 05.5' S./18° 17.3' E. in 27 metres on white sand. Among them were numerous mature males and ovigerous females. Ten specimens were selected as the types and one of these, a mature male measuring 9 mm. by 0.4 mm. for 90 segments is designated the holotype. The anterior part of the body is colourless but from segment 60 it is swollen and white with sperm.

The proboscis is extruded and shows a small dorsal tooth. The pharynx when retracted would continue back to setiger 9 and the proventriculus which has 35 rows of points is the same length as the pharynx. The prostomium (Text-fig. 4 *k*) is broader than long with 2 pairs of small eyes. The antennae are slender and clearly annulated, the median which is posterior in origin having 14 long joints and the laterals having 12. The palps are broad and separate at the base. There is no occipital flap.The tentacular cirri and dorsal cirri (Text-fig. 4 *l*) are essentially similar, all slender with 12-14 long joints and equal to two-thirds of the segmental breadth. Posterior cirri are shorter and have only 10-12 joints but they are never stout and fusiform as in *S. armillaris*. The ventral cirri are rather long and project beyond the setigerous lobes.There are two knobbed acicula per parapodium and about 6 compound setae. Each of these (Text-fig. 4 *m*) has a straight unidentate blade of normal length. A simple needlelike superior seta appears in the last few feet.This species is obviously close to *S. armillaris* and agrees with it in having unidentate setae. However, the dorsal cirri are quite different, for in contrast to the short fusiform dorsal cirri of *S. armillaris* the cirri of *S. benguellana* are filiform, with 10-14 elongated joints. Holotype: B.M.(N.H.), Reg. No. 1963.1.50.*Eusyllis assimilis* Marenzeller, 1875*Eusyllis assimilis* Marenzeller, 1875: 158; Fauvel, 1923: 294, fig. 112 *a-g*.*Eusyllis monilocornis*: Fauvel 1923*a*: 6.

RECORDS. WCD 41 (1), 87 (1).

NOTES. *E. assimilis* was recorded from southern Angola by Fauvel (1923*a*) under the name of *E. monilicornis*. Fauvel's statement that the bidentate setae have both long and blades shows that his record refers to *E. assimilis* and not *E. blomstrandii*.

This is the first record from South Africa.

***Anguillosyllis* gen. n.**

Prostomium with 3 minute antennae and a pair of large pointed palps fused for half their length. A single pair of minute tentacular cirri. Pharynx straight, unarmed. Dorsal cirri long but not annulated. Ventral cirri present. Setigerous lobe of the parapodium with a contractile dorsal projection.

Setae compound and falcigerous.

TYPE SPECIES. *Anguillosyllis capensis* Day, 1963.

***Anguillosyllis capensis* sp. n.**

(Text-fig. 5 *a-d*)

RECORDS. SCD 275 (2) ; WCD 106 (1).

DESCRIPTION. The type material consists of two incomplete specimens from station SCD 275 dredged at 34° 51' S./23° 41' E. in 183 metres on fine sand. One is extended and measures 3.5 mm. for 12 segments and the other is contracted and measures 2.5 mm. for 13 segments. The description given below is based on the extended specimen which is designated the holotype.

The head end (Text-fig. 5 *b*) is pointed due to the tapered palps which project well forward and are fused for over half their length. The prostomium is oval and broader than long. There are no eyes but three short club-shaped antennae are present with the median further back than the two laterals and difficult to see. The peristome bears a single pair of lateral tentacular cirri which are rather smaller than the antennae.

The pharynx when dissected proved to be short, broad and straight and reached setiger 3. Careful dissection failed to reveal the dorsal tooth which was expected and the whole pharynx is smooth. The pharyngeal sheath appears to have 6 soft papillae. The proventriculus is barrel-shaped and extends through setigers 4, 5 and 6 and has about 30 rows of points.

The segments and parapodia are similar throughout. Each segment is more than twice as broad as long and each parapodium (Text-fig. 5 *c*) has a long dorsal cirrus, a characteristic setigerous lobe and a slender ventral cirrus. The dorsal cirrus is very long and slender, without any sign of annulation and is usually twisted and coiled. The setigerous lobe is well developed with a dorsal hood over the setae which tapers to a cirriform projection. When retracted (Text-fig. 5 *d*) the dorsal hood is no longer obvious and the end of the setigerous lobe then appears to have three lips ; one superior, one anterior and one posterior. The ventral cirrus is slender and arises from the distal end of the setigerous lobe just below the setae.

The setae (Text-fig. 5 *a*) are very numerous and all similar. Each is compound and falcigerous with a rather long, minutely serrated blade and a blunt unidentate tip.

The fusion of the palps and the presence of a single pair of tentacular cirri place this species in the sub-family *Exogoninae* ; further the well developed dorsal cirri suggest that it is closer to *Sphaerosyllis* than *Exogone*. But it is obviously distinct

from both these genera. The lack of a dorsal tooth on the pharynx is unusual and the curious dorsal hood over the parapodium is unique. Holotype: B.M.(N.H.) Reg. No. 1963.1.29.

Exogone normalis sp. n.

(Text-fig. 5 *e-h*)

RECORDS. SCD 130 (3), 212 (2), 215 (1); FAL 419 (3).

DESCRIPTION. The type material consists of three specimens from station SCD 130 obtained by a van Veen grab at 34° 48' S./22° 06' E. in 100 metres on a sandy bottom on 3rd June, 1960. The largest specimen measuring 5.5 mm. by 0.3 mm. for 50 segments is designated the holotype. The paratypes are slightly smaller. All are creamy brown in alcohol.

The palps (Text-fig. 5 *g*) are large, about three times as long as the prostomium and broader basally. They are completely fused dorsally but broadly grooved ventrally. The prostomium is three times as broad as long with three pairs of large eyes which are coalescent on each side in the holotype but there are only two pairs of small eyes in the two paratypes. The three antennae arise close together on the posterior margin of the prostomium. The median is longer than the prostomium and reaches the base of the palps but the laterals are very small, only one-third the length of the median. The pharynx has a single dorsal tooth and extends back to setiger 5. The proventriculus which is the same length extends on to setiger 10 and has about 23 rows of points.

The tentacular segment is about the same length as the prostomium and quite distinct from it. There is a nuchal organ at the junction between the prostomium and peristomium and the latter bears a single pair of very small tentacular cirri which are only half the size of the first pair of dorsal cirri.

The body is cylindrical and quite smooth. The parapodia (Text-fig. 5 *h*) are bluntly conical lateral projections. The dorsal cirri are small ovoid papillae well above the parapodia. There is no dorsal cirrus on setiger 2. The ventral cirri are twice the length of the dorsal cirri and project beyond the ends of the parapodia.

Anterior segments bear 12 setae but the number is reduced to about 5 posteriorly. The first 9 segments bear compound setae only, then a superior simple seta appears and finally, in the last few segments an inferior simple seta as well. All the compound setae (Text-fig. 5 *f*) are similar with moderate shaft-heads and straight unidentate blades of normal length. It is emphasised that there is no specialised superior compound seta. The superior simple seta (Text-fig. 5 *e*) is a straight blunt needle which gradually increases in thickness until, in posterior segments it is twice the diameter of the compound setae. The inferior seta is the same diameter as the compound seta.

The pygidium bears a pair of anal cirri. Holotype: B.M.(N.H.), Reg. No. 1963.1.30.

Three species of *Exogone* have been recorded from South Africa and there is a very doubtful record of the Antarctic species *E. heterosetosa* from Madagascar. *E. clavator* Ehlers and *E. verugera* Claparède both have dorsal cirri on setiger 2 and

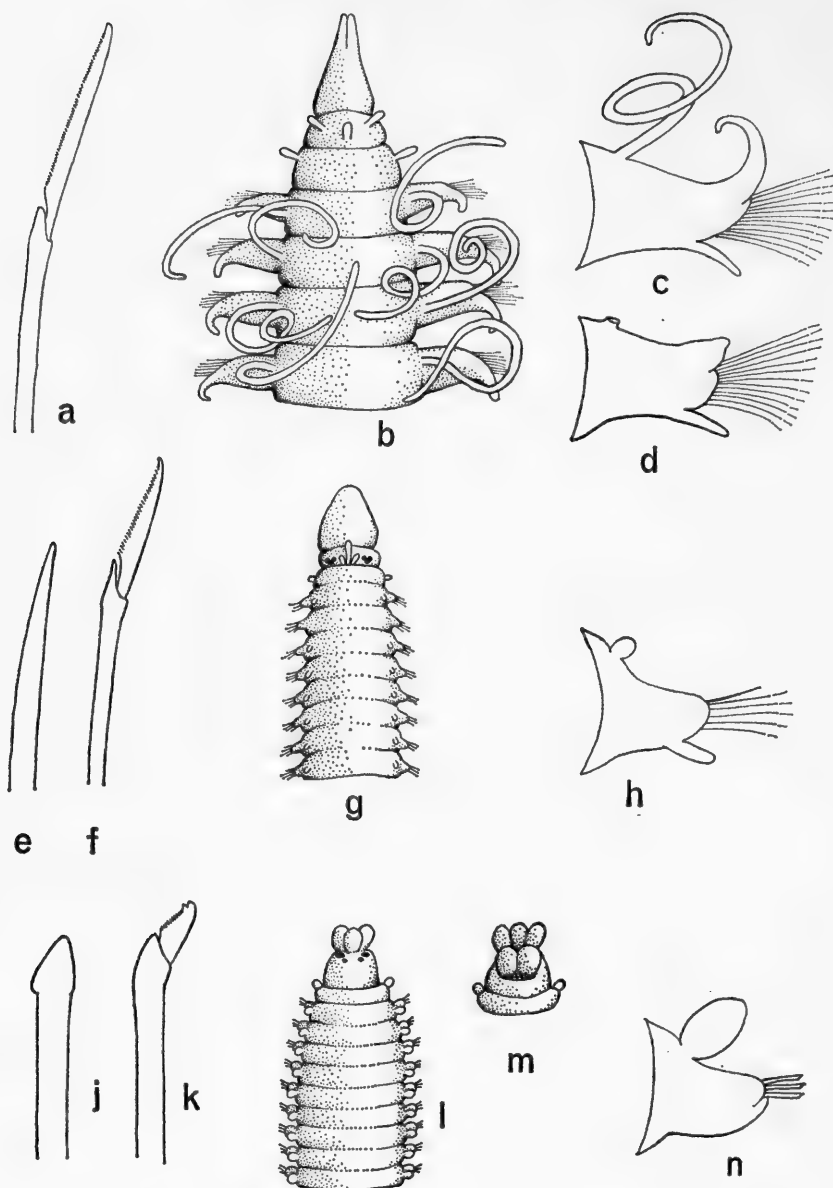


FIG. 5. *Anguillosyllis capensis*: (a) seta; (b) anterior end; (c) expanded parapodium; (d) contracted parapodium with dorsal cirrus omitted. *Exogone normalis*: (e) superior simple seta; (f) compound seta; (g) anterior end; (h) parapodium. *Exogonoides antennata*: (j) simple seta; (k) compound seta from 2nd foot; (l) dorsal view of anterior end; (m) ventral view of head; (n) parapodium.

both have a superior compound seta with a long swordlike blade. *E. heterosetosa* McIntosh and *E. gemmifera* Pagenstecher both lack a dorsal cirrus on setiger 2 and in this respect they agree with *E. normalis* but their setae differ. Their normal

compound setae are bidentate and both have a specialised superior compound seta. In *E. heterosetosa* it has a very swollen shaft-head and a broad triangular blade and in *E. gemmifera* it has a normal shaft-head and a long swordlike blade.

Exogonoides gen. n.

Prostomium with three ovoid frontal antennae. Palps small, ventral, partially fused. Pharynx straight without obvious teeth. Proventriculus poorly developed. A single pair of small tentacular cirri. Dorsal cirri ovoid. Ventral cirri absent (fused to setigerous lobe). Setae compound anteriorly but simple posteriorly.

TYPE SPECIES. *E. antennata* Day, 1963.

Exogonoides antennata sp. n.

(Text-fig. 5 *j-n*)

RECORDS. SCD 246 (2).

DESCRIPTION. The type material was dredged at station SCD 246 at 34° 02' S./23° 28' E. in 49 metres on sand, mud and rock. One of the two specimens has a damaged head. The other, measuring 35 mm. by 0.5 mm. for over 200 segments is designated the holotype. It is creamy brown in alcohol and lacks colour markings. The general appearance is that of a very long *Exogone*, hence the name.

The prostomium (Text-fig. 5 *l*) is bluntly conical with three stout ovoid antennae projecting forward from the anterior end, the median being superior to the two laterals. There are two pairs of eyes of which the anterior pair is larger and wider apart than the posterior pair. The palps (Text-fig. 5 *m*) are small and not visible dorsally. They arise from the antero-ventral margin of the prostomium as two cushion-like lobes in contact with one another. While they are obviously not fused completely it is impossible to say that they are entirely separate and it is presumed that they are partially fused. The pharynx and proventriculus when dissected proved to be slender and attached by mesenteries throughout. Even when the pharynx was removed and cleared, no teeth or trepan was seen and it is thought to be unarmed. The pharynx which extends back to setiger 6 is straight anteriorly but somewhat sinuous where it meets the proventriculus which is small, dark and unusually thin walled. About 15 rows of lumps corresponding to the "points" of a normal gizzard were seen.

The tentacular segment is as long as the body segments and bears a single pair of small ovoid tentacular cirri similar to those found in the genus *Exogone*. There is no sign of a second pair.

The body is very long and slender, anterior segments being about 8 times as broad as long but posterior ones are longer, only twice as broad as long. The body surface is quite smooth.

The parapodia (Text-fig. 5 *n*) are similar throughout. The dorsal cirrus is ovoid in outline, somewhat compressed and about half the size of the setigerous lobe. The setigerous lobe itself is a broad lateral projection with the ventral cirrus completely fused to the postero-ventral margin so that ventral cirri may be said to be

absent as in the *Autolytinae*. The setae are usually three in number and most of them are simple spines with bluntly triangular tips. However, in the first few feet the setae (Text-fig. 5 *k*) bear short, triangular bidentate blades so that the later simple setae (Text-fig. 5 *j*) are obviously homologous with the shafts of the anterior compound forms.

This species cannot be assigned to any known genus. The single tentacular cirrus and short ovoid antennae and cirri are reminiscent of *Exogone* but the latter has completely fused palps projecting forwards, the antennae are dorsal not terminal, and there is a well marked dorsal tooth and distinct ventral cirri. In these respects the present species is related to the *Autolytinae* but the latter has two pairs of tentacular cirri. It is suggested that the subfamily *Autolytinae* be enlarged to include forms with one pair of tentacular cirri and the new genus *Exogonoides* be included in it. Holotype: B.M.(N.H.), Reg. No. 1963.1.34.

Family NEREIDAE

Micronereides gen. n.

Small Nereidae generally similar to *Micronereis* but possessing two antennae. Proboscis without paragnaths but with a pair of toothed jaws. Prostomium with a pair of antennae and a pair of biarticulate palps. Two pairs of tentacular cirri. No apodous segment behind the peristome. First two segments uniramous, subsequent ones biramous. Setae are all homologous spinigers.

TYPE. *Micronereides capensis* Day.

Micronereides capensis sp. n.

(Text-fig. 6 *a-e*)

RECORDS. SCD 233 (1).

The holotype is a single specimen measuring 6 mm. for 34 segments. It was dredged at Station SCD 233 position 36° 28.5' S./21° 11' E. on the Agulhas Bank in 183 metres on a bottom of fine sand. There is no colour pattern. The prostomium (Text-fig. 6 *b*) is broad, almost square with the eyes either indistinct or absent. A pair of widely separated antennae is present. The palps have stout palpophores completely fused to the prostomium and slender palpostyles longer than the antennae. The proboscis lacks paragnaths but has a pair of large jaws with 7 teeth. There are two pairs of short tentacular cirri arranged 2:2 showing that they have been derived from two fused segments. There is no anterior apodous segment. The first two setigerous segments are uniramous, the notopodial lobes and notosetae being absent though the dorsal cirrus remains. Subsequent segments have biramous parapodia which are similar in structure throughout. The pygidium is unknown.

Normal parapodia (Text-fig. 6 *c*) are deeply cleft between the notopodia and neuropodia. The dorsal cirrus is rather short and the superior lobe of the notopodium is absent. The inferior lobe of the notopodium however, is elongated and

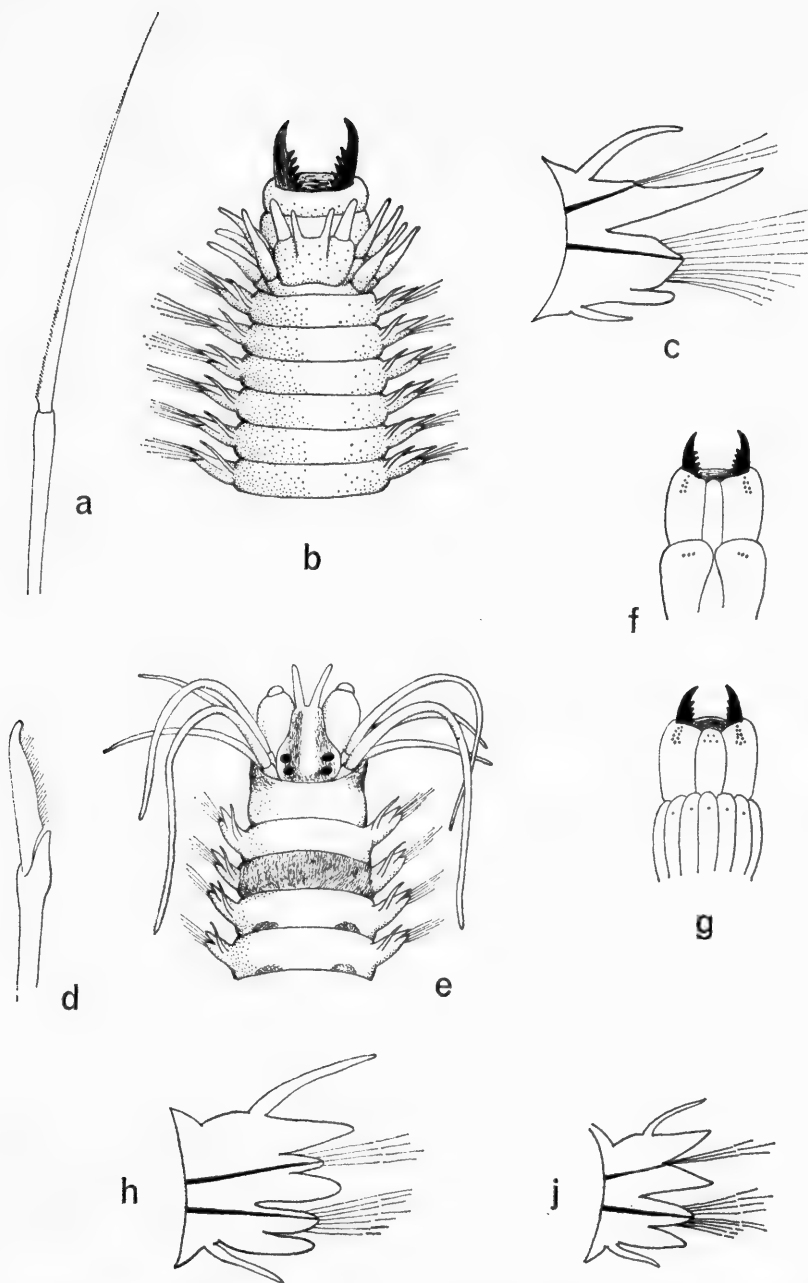


FIG. 6. *Micronereides capensis*: (a) seta; (b) anterior end; (c) parapodium. *Nereis* (*Neanthes*) *agulhana*: (d) falcigerous neuroseta; (e) anterior end; (f) dorsal view of proboscis; (g) ventral view of proboscis; (h) roth foot; (j) posterior foot.

exceeds the dorsal cirrus. There is no intermediate (setigerous) lobe. The neuropodium consists of a stout, conical setigerous lobe, a very small inferior lobe and a small ventral cirrus.

The setae (Text-fig. 6 *a*) are all homogomph spinigers though the inferior series in the neuropodia have rather short blades and the shaft-heads might be considered hemigomph.

REMARKS. The new genus *Micronereides* is obviously close to *Micronereis* Claparède, 1863 in which Hartman (1959) recognised three species, *M. halei* Hartman, 1954 from South Australia, *M. nanaimoensis* Berkeley and Berkeley, 1953 from Western Canada and *M. variegata* Claparède, 1863 from France.

I have not seen a description of *M. nanaimoensis* but the other two species both lack antennae and it would seem unwise to enlarge the generic description of the well established genus *Micronereis* to include forms with two antennae. Holotype: B.M.(N.H.), Reg. No. 1963.1.60.

Nereis (Neanthes) agulhana sp. n.

(Text-fig. 6 *d-j*)

Nereis (Neanthes) cf. *keruelensis*: Day, 1960: 321.

RECORDS. SCD 156 (3), 182 (4), 207 (6 juvs.), 237 (1 juv.), 246 (1).

The holotype is a specimen measuring 20 mm. with 65 segments selected from the material dredged at station SCD 156 at 34° 03' S./25° 59' E. in 84 metres on a rocky bottom. The colour in alcohol is pale with touches of brown on the prostomium, a well marked and characteristic bar across the dorsum of setiger 2 and a pair of small spots on each of the succeeding anterior segments (see Text-fig. 6 *e*).

The antennae and tentacular cirri are rather long and slender and the prostomium itself is longer than broad.

The proboscis (Text-figs. 4 *f* and *g*) has group I = 0; II = 8-9 in a double row; III = a group of 5-6; IV = a wedge of 8-12; V = 0; VI = 2-4 close-set points in a transverse line; VII and VIII = a single row of 3-5.

Anterior feet (Text-fig. 6 *h*) have pointed lobes and slightly longer dorsal cirri. The notopodium has three lobes, the middle lobe bearing the notosetae being well marked but obviously smaller than the other two. The setigerous lobe of the neuropodium has no projecting presetal or postsetal lips.

In posterior feet (Text-fig. 6 *j*) the dorsal cirrus is rather smaller and the notopodium has lost its third or setigerous lobe. The two notopodial lobes that remain are stout, markedly pointed and divergent. The structure of the neuropodium is the same as in the anterior feet.

The notosetae are homogomph spinigers throughout, there being no notopodial falcigers. The neurosetae include the normal series of homogomph and heterogomph spinigers and heterogomph falcigers. The latter (Text-fig. 6 *d*) have rather straight blades with a tendon attached to the blunt tip.

This species is close to *N. keruelensis* McIntosh, 1885 which has now been reported from many parts of the world including the Mediterranean. However an examination of McIntosh's type in the British Museum (Reg. No. 1885: 12: 1: 170) and

other specimens identified as *N. kerguelensis* from sub-antarctic localities by Monro, 1930 shows that the South African material is distinct.

In the type of *N. kerguelensis* the proboscis has group I with 2 points in line, V = 0, VI a single small point and VII and VIII a row of 5 points. The prostomium is broad, almost oval, and the colour of the body is uniformly pale. In anterior feet the third (setigerous) lobe of the notopodium is small and the setigerous lobe of the neuropodium has a prominent, almost digitiform postsetal lip. This is not shown in McIntosh's pl. 35, fig. 11 but it is quite distinct in the type, and is referred to by Monro, 1930. Holotype: B.M.(N.H.), Reg. No. 1963.1.61.

In brief the important differences between *N. agulhana* which is apparently common in deep water dredgings around South Africa and the sub-antarctic *N. kerguelensis* concern the distribution of paragnaths, the presence of a brown bar across setiger 2 which is present in every specimen of *N. agulhana*, the structure of the setigerous lobe of the neuropodium and according to Ramsay (1914) and Monro (1936) the lack of heterogomph spinigers in the neuropodia of *N. kerguelensis*.

N. papillosa Day 1963 has a similar arrangement of paragnaths but is immediately separated by the presence of papillae on the parapodial lobes of middle feet.

Family SPHAERODORIDAE

Sphaerodorum benguellarum sp. n.

(Text-fig. 7 a-c)

RECORDS. WCD 110 (1).

DESCRIPTION. The type locality is 32° 08' S./17° 39' E. in 172 metres. The single specimen (Text-fig. 7 b) is ovoid, 2.2 mm. long by 0.8 mm. broad with 24 segments. The head is retracted and its appendages are not visible, but a pair of dark eyes was seen on clearing with glycerine. There is a large muscular gizzard.

The whole body is covered with papillae. Each segment has an anterior row of 8 large papillae across the dorsum and a posterior, more irregular row of about 20 small papillae. The papillae above and below the parapodia are not larger than the rest. The parapodia themselves (Text-fig. 7 c) are wrinkled and obviously retractile. Each is conical in shape with a large presetal papilla, about 12 setae and two smaller postsetal papillae.

The setae (Text-fig. 7 a) are all compound, each with a swollen shaft-head and a long tapered falcigerous blade. The tip is minute but probably unidentate. Holotype: B.M.(N.H.), Reg. No. 1963.1.75.

Sphaerodorum capense sp. n.

(Text-fig. 7 d-f)

RECORDS. CP 452—1 specimen found among *Gunnarea* tubes on the shore at Mouillé Point, Cape Town on 1st October, 1955.

DESCRIPTION. The holotype (Text-fig. 7 d) is ovoid in shape 2.5 mm. long, 0.8 mm. wide and has 16 setigers. The colour is yellowish, with a pair of black eyes

and the dark contents of the gut showing through the skin. The head is retracted and its appendages are indistinguishable from the numerous spherical papillae which cover the whole surface.

Each body segment has two transverse rows of papillae across the dorsum. The anterior row consists of about 18 larger papillae and the posterior irregular row has many more smaller ones about half the size of those in the anterior row. The papillae above the parapodia are not obviously enlarged as in *S. gracile*. The parapodia (Text-fig. 7 f) are small, obviously retractile and covered with papillae with a larger one apically. There are about 10 long setae per parapodium. Each seta (Text-fig. 7 e) is compound with a broad oval shaft-head and an indistinctly separated blade ending in a small, hooked unidentate tip. *S. capense* may be distinguished from other species of the genus by the characteristic setae and the distribution of the papillae. Holotype : B.M.(N.H.), Reg. No. 1963.1.74.

Family GLYCERIDAE

Goniadella gracilis (Verrill, 1873)

Eonè gracilis Verrill, 1873 : 596.

Goniadella gracilis : Hartman, 1950 : 42, pl. 5, figs. 4-8.

RECORDS. FAL 413 (3) ; SCD 212 (1), 218 (6), 237 (2), 245 (1), 275 (3), 288 (1).

NOTES. This small threadlike species which averages 10-15 mm. in length seems to be common in grab samples around the Cape. The genus *Goniadella* is close to *Goniada* but may be distinguished by the possession of both falcigerous and spinigerous neurosetae instead of spinigers alone. *G. gracilis* (Verrill) is the only species known and the long digitiform presetal lip on the neuropodium is characteristic. The South African specimens differ from Hartman's description only in a few minor points. The proboscis has about 30 chevrons at its base, instead of 25, no eyes were found on the terminal ring of the prostomium, only on the basal one and there are fewer notosetae in posterior segments.

Family EUNICIDAE

Subfamily EUNICINAE

Marphysa purcellana Willey, 1904

Marphysa purcellana Willey, 1904 : 263, pl. 13, fig. 17 ; Day, 1953 : 435.

RECORDS. Seven specimens obtained by a dredger prospecting for diamonds north of the Orange River mouth in about 5-10 fathoms.

NOTES. This is a new record for South West Africa.

Subfamily ONUPHIDINAE

Diopatra dubia Day, 1960

Diopatra dubia Day, 1960 : 348, fig. 10 g-h.

RECORDS. SCD 288 (1)

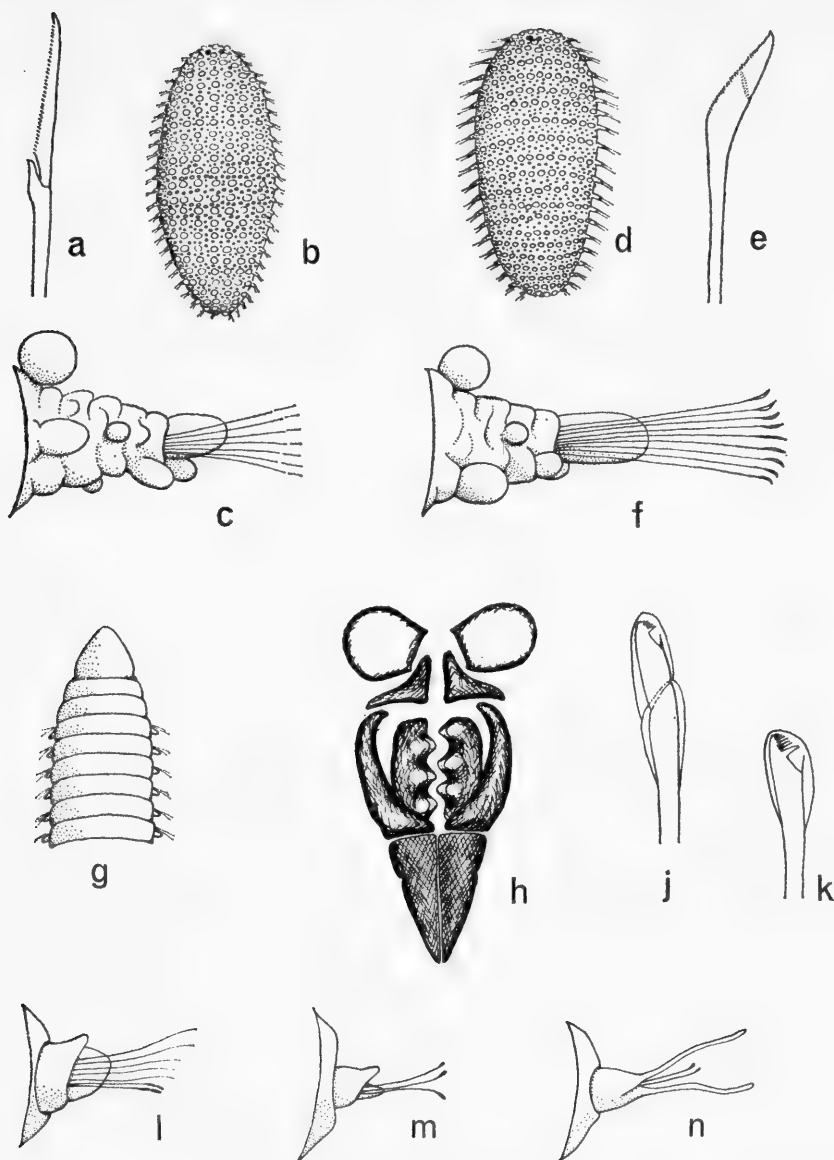


FIG. 7. *Sphaerodorum capense*: (a) seta; (b) entire worm; (c) parapodium. *Sphaerodorum benguellarum*: (d) entire worm; (e) seta; (f) parapodium. *Lumbrineris meteorana*: (g) anterior end; (h) maxillae (j) compound hook; (k) simple hook; (l) anterior view of 6th foot; (m) anterior view of 50th foot; (n) anterior view of far posterior foot.

NOTES. Although this species seems to be widely distributed on the Atlantic coast of South Africa and is fairly common in False Bay, this record extends its range to the Indian Ocean off East London.

***Onuphis quinquedens* Day, 1951**

Onuphis quinquedens Day, 1951 : 40, fig. 6 a-h.

RECORDS. Muizenberg beach (locally common).

NOTES. This species has not been seen since its original discovery in Zululand. The new record extends its known range to False Bay. It is apparently common in a small area at the sheltered western end of Muizenberg bathing beach where it burrows in sand near low tide. The new specimens are much larger than the holotype and reach a length of 350 mm. by 8 mm. The notch between the tentacular cirri is distinctive.

Subfamily **LUMBRINERINAE*****Lumbrineris heteropoda difficilis* nom. nov.**

Lumbrineris heteropoda difficilis nom. nov. pro *Lumbrineris heteropoda* var. *atlantica* (non *Lumbriconereis atlantica* Kinberg, 1865 : 568 ; Fauvel 1934 : 27) Day, 1960 : 360, fig. 12 c-d. *Lumbriconereis heteropoda* : Monro, 1930 : 137 ; Monro, 1936 : 154.

RECORDS. WCD 90 (2 + 2 juvs.), 94 (2 + 3 juvs.), 103 (12), 121 (2).

NOTES. This subspecies differs from *L. heteropoda* in the extreme length of the posterior feet and the possession of dark acicula. Its relationship to *L. h. heteropoda* has been discussed by me (Day, 1957, 1960) under the name *L. heteropoda* var. *atlantica*. Hartman (1959) showed that the name *atlantica* has been used both by Kinberg, 1865 and Fauvel, 1934 so that these South African specimens must be renamed.

***Lumbrineris meteorana* (Augener, 1931)**

(Text-fig. 7 g-n)

Lumbriconereis meteorana Augener, 1931 : 300, fig. 8 a-e (partim).

Lumbrineris cf. *meteorana* : Day 1960, p. 358.

RECORDS. WCD 60 (4), 61 (5), 63 (28), 64 (11), 66 (8), 67 (1), 97 (3), 109 (13), 112 (3 + 10 juvs.), 115 (1 + 3 juvs.) ; FAL 390 (43) ; SCD 185 (1), 187 (15), 193 (4), 197 (13), 200 (14), 214 (3 juvs.).

DESCRIPTION. The abundant material now available has confirmed the suspicion expressed by me (Day, 1960) that the two fragments described by Augener (1931) do not belong to the same species. I suggest that the name *L. meteorana* should be restricted to the posterior fragment with its characteristically long filamentous parapodial lobes. A summarised description of a complete specimen from station WCD 60 is given below.

Body slender, about 20 mm. long by 0.8 mm. broad with 120 segments. Yellowish white in alcohol. Prostomium (Text-fig. 7 g) bluntly conical. Mandibles weak, and poorly calcified with shafts in contact throughout their length. Maxillary formula : I = 1 + 1 ; II = 3 + 3 ; III = ?1 + ?1 ; IV = 1 + 1. The maxillary supports (Text-fig. 7 h) are broadly triangular, the main fangs (Mx. I) are weakly

chitinised and blunt, each of the main dental plates (Mx. II) has three blunt bilobed teeth, Mx. III are cutting plates with a sharp edge but no definite tooth while Mx. IV are large and rounded, each with pale centre and a dark edge on which there is an indistinct tooth.

Anterior feet (Text-fig. 7 *l*) have rather flattened lobes, the low presetal one being more developed superiorly while the larger postsetal one is compressed and bluntly rounded. In the middle feet (Text-fig. 7 *m*) the two lobes are both small and subequal. This condition persists over most of the body but near the posterior end the two parapodial lobes (Text-fig. 7 *n*) elongate and become filamentous; as always the presetal one is slightly more superior than the postsetal.

The acicula are pale in all feet. Anterior setae include about 4 winged capillaries and 2 compound hooks. The hooks are compound (Text-fig. 7 *j*) for the first 10–15 feet but then become simple with short hoods and unusually long teeth (see Text-fig. 7 *k*). One or two such hooks persist to the end of the body.

The capillaries decrease in number after the first few feet and disappear before the middle of the body.

This species differs from *L. bifilaris* Ehlers in the structure of the maxillae and in the possession of jointed hooks anteriorly. In both characters it is close to *L. albidentata* but the posterior feet are quite different and the mandibular shafts are in contact throughout, not widely divergent as in *L. albidentata*.

***Lumbrineris aberrans* sp. n.**

(Text-fig. 8 *a–f*)

RECORDS. SCD 212 (1).

DESCRIPTION. The type locality is 33° 58.8' S./25° 42.2' E. in 26 metres. The single specimen is 6 mm. long with 38 setigers but is incomplete posteriorly. The anterior end however is quite characteristic.

The prostomium (Text-fig. 8 *a*) is enormously elongated, conical and about as long as the combined length of the first two apodous segments plus the first four setigers. The mandibles (Text-fig. 8 *c*) are small and lightly chitinised. The maxillary supports (Text-fig. 8 *b*) are very long and triangular and the maxillary formula is Mx. I = 1 + 1; II = 3 + 3; III ?1 + ?1 (short plates with one indistinct tooth); IV = 0 + 0 (oval plates without teeth).

The first two apodous segments are short and the first few setigerous segments that follow have such small parapodial lobes that the setae appear to arise from the sides of the segments. The first well formed parapodium is on setiger 7 and from there on the parapodial lobes increase in size though they are never large. Within the 38 setigers investigated all the parapodia (Text-fig. 8 *e*) are essentially similar in shape. Each has a low rounded presetal lobe and a small digitiform postsetal lobe always shorter than the setae. There are 4–6 setae per parapodium. Capillaries appear in the first setiger and simple hooks in the fourth. The first few capillaries have very short broad blades but they become longer and more tapered posteriorly (see Text-fig. 8 *d*). The hooks (Text-fig. 8 *f*) have short broad hoods and are distinctive in having only two stout teeth instead of the usual series of one large and several small ones. The acicula are pale.

This species is obviously related to *L. acuta* Verrill, 1875 from Rhode Island, U.S.A. and *L. mucronata* Ehlers, 1908 from the mouth of the Congo. The former lacks hooks but the latter is closer for it also has bidentate hooks. However, in *L. mucronata* the prostomium is relatively shorter, the maxillary supports narrower and maxillary formula is different. Ehlers was only able to see the maxillae by transparency in a cleared preparation but he figures Mx. II with 6 teeth and Mx. IV with about 8 small ones. Both of these features are unusual and dissection may show that Ehlers' interpretation was inaccurate. If so, *L. aberrans* may prove to be a synonym of *L. mucronata*. Holotype: B.M.(N.H.), Reg. No. 1963.1.86.

Subfamily ARABELLINAE

Drilonereis falcata Moore, 1911

Drilonereis falcata Moore, 1911: 298; Day, 1960: 364, fig. 13 a-e.

RECORDS. One specimen obtained by a dredger prospecting for diamonds north of the Orange River mouth in 5-10 fathoms.

NOTES. This is a new record for South West Africa.

Subfamily DORVILLEINAE

Protodorvillea egena (Ehlers, 1913)

Stauronereis egena Ehlers, 1913: 501, pl. 35, figs. 1-6.

Non *Stauronereis egena*: Augener, 1918: 377, pl. 5, figs. 102-103, fig. 45.

Dorvillea egena Day, 1960: 371.

Protodorvillea egena Pettibone, 1961: 180.

RECORDS. FAL 284 (1).

NOTES. The discovery of a specimen from the type locality (False Bay) allows me to confirm Ehlers' description apart from minor points. The present specimen is 5.0 mm. long and thus slightly larger than the 4.5 mm. holotype. Only the second large pair of eyes is visible, not the anterior minute pair. As stated by Ehlers the short antennae consist of a single club-shaped joint, there is no dorsal cirrus on setiger 1 but small ovoid dorsal cirri without cirrophores or internal acicula are present on all subsequent feet. The presetal lobe projects well beyond the postsetal one. The superior simple setae include 1-2 forked setae with subequal prongs and smooth shafts and 1-2 capillaries which appear smooth under low power but are actually faintly serrate at the base of the blade. The inferior compound setae number 3-4 per bundle. The blades vary in length, some being as long as that figured by Ehlers (pl. 35, fig. 4) but others much shorter. They are all falcigerous and under high power it may be seen that the tip is minutely bidentate.

Augener's specimens from South West Africa were considerably larger (9-16 mm.) with multi-articulate antennae, the dorsal cirri are reported to be mounted on cirrophores and the forked setae are shown (Text-fig. 45 a) as having unequal prongs and serrations on one side of the shaft-head.

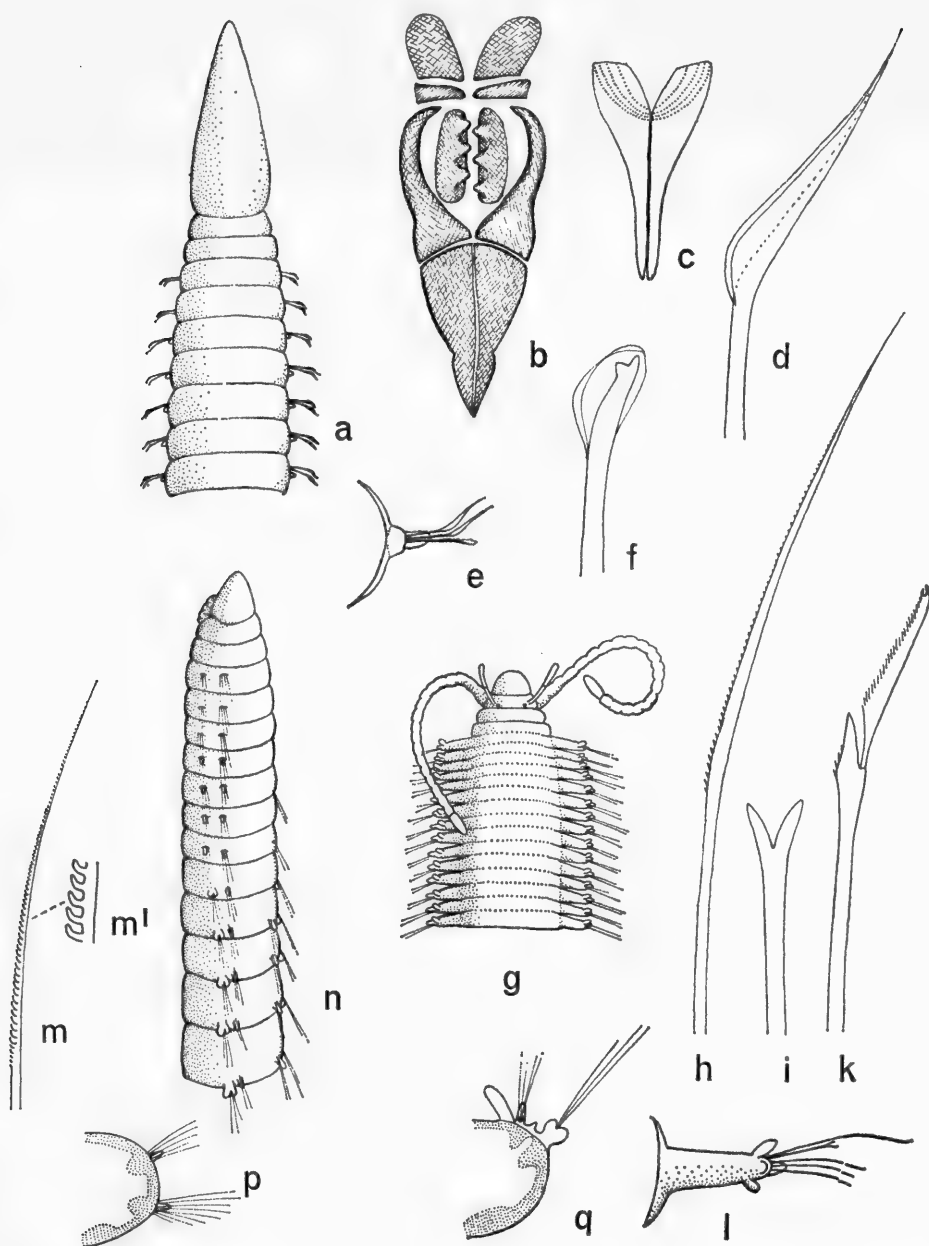


FIG. 8. *Lumbrineris aberrans* : (a) anterior end ; (b) maxillae ; (c) mandibles ; (d) capillary seta from 20th foot ; (e) anterior parapodium ; (f) hook. *Protodorvillea biarticulata* : (g) anterior end ; (h) superior capillary seta ; (i) forked seta ; (j) compound seta ; (l) posterior view of parapodium. *Scoliolella capensis* : (m, m') thoracic neuroseta and details of crenulations ; (n) dorso-lateral view of head and first twelve setigers ; (p) 6th foot ; (q) 24th foot.

***Protodorvillea biarticulata* sp. n.**

(Text-fig. 8 g-l)

RECORDS. SCD 140 (2), 213 (3).

DESCRIPTION. The holotype is a complete specimen measuring 4.0 mm. by 0.3 mm. for 100 segments. It was obtained by grab from station SCD 140 at 34° 35' S./21° 56' E. in 78 metres on a bottom of broken shell. The specimen is colourless in alcohol.

The two-ringed prostomium (Text-fig. 8 g) is smoothly ovoid anteriorly and has a single pair of posterior eyes. The palps are long and coiled with irregularly annulated or wrinkled palpophores and rather long oval palpostyles. They reach back to setiger 10. The antennae are a little shorter than the length of the prostomium and are biarticulate with two long joints. The mandibles and maxillae were not clearly seen but appear to be normal. There are two apodous segments behind the prostomium.

The body is somewhat flattened and consists of 100 short segments each about 8 times broader than long. The parapodia (Text-fig. 8 l) are relatively large. They are the same width as the segments and extend outwards for a distance equal to half the body width. Each one, including the first is provided with a small ovoid dorsal cirrus without a cirrophore or internal aciculum. The setigerous lobe has a blunt projecting presetal lobe longer than the dorsal cirrus, a very short postsetal lobe or lip and a ventral cirrus similar to the dorsal one.

There are 5-6 setae. Superiorly there is a forked seta and a simple capillary and inferiorly there are 3-4 compound setae. The forked seta (Text-fig. 8 j) has a smooth shaft-head and subequal prongs which are flanged but not serrated on their inner margins. The capillary seta (Text-fig. 8 h) has a narrow blade serrated basally, while the compound setae (Text-fig. 8 k) are falcigerous with shaft-heads which are minutely serrated on one side and blades which vary in length and end in minutely bidentate tips.

The pygidium bears two pairs of long cylindrical anal cirri.

Pettibone (1961) has recently revised the Dorvilleidae in which she recognises five genera. Her new genus *Protodorvillea* resembles *Ophryotrocha* in having uniramous parapodia and lacking dorsal cirrophores but may be distinguished from it by the characters of the jaws, and by the possession of longer jointed palps and forked setae. According to her species key the present species is most closely related to *P. kefersteini* (McIntosh) and *P. gracilis* (Hartman) and may be distinguished from *P. egena* (Ehlers) by the presence of dorsal cirri on the first setiger and (one might add) the possession of two-jointed antennae. *P. gracilis* (Hartman, 1938) from California has single-jointed antennae and the pre- and postsetal lobes of the parapodia are very short and subequal. *P. kefersteini* (McIntosh, 1869) from Europe as re-described by Fauvel, 1923 is a larger species up to 15 mm. long with possibly 4 indistinct annulations on the antennae and broad, subequal pre- and postsetal lobes to the parapodia. Holotype: B.M.(N.H.), Reg. No. 1963.1.87.

***Ophryotrocha puerilis* Clap. & Mecz., 1869**

Ophryotrocha puerilis Claparède & Mecznirow, 1869: 184; Fauvel, 1923: 450, fig. 180 a-h; Hartman, 1944: 191, pl. 15, figs. 325-330.

RECORDS. Specimens numerous in aquaria in Cape Town in June and August, 1962.

NOTES. The specimens are quite typical. Dissection of the maxillae showed that there are 7 pairs of small dentate elements attached to a pair of chitinous strands leading back to the main fangs. The 3 proximal pairs are dark and have about 5 teeth of decreasing size and the 4 distal pairs are pale and have about 12 minute subequal teeth. These are used in the same way as a radula to scrape off attached diatoms which fill the gut. Specimens were found breeding in August. This is the first record of this cosmopolitan species from South Africa.

Family ORBINIIDAE**Subfamily PROTOARCIINAE*****Scolopella* gen. n.**

Small *Oribiniidae* belonging to the sub-family *Protoariciinae* with two achaetous segments following the prostomium. Thoracic region with few segments. Thoracic setae are crenulate capillaries in both rami. Abdominal region with both notopodial and neuropodial lobes bearing capillary seta. No specialised setae. Branchiae restricted to the abdominal segments.

TYPE SPECIES. *Scolopella capensis* Day.

***Scolopella capensis* sp. n.**

(Text-fig. 8 m-q)

RECORDS. WCD 79 (2), 116 (3); SCD 237 (2).

DESCRIPTION. The type material comes from station WCD 116 at 33° 06.5' S./17° 32.9' E. in 183 metres on a bottom of dark green mud. There are two incomplete specimens. The holotype measures 15 mm. by 0.3 mm. for 48 segments while the paratype measures 8 mm. for 25 segments. All are rounded in section and quite pale in alcohol.

The prostomium (Text-fig. 8 n) is bluntly conical and lacks eyes. The proboscis is retracted so that it is not possible to say whether its distal end is lobed or smooth.

The body is roughly cylindrical in section without any obvious flattening of the anterior region. The first 9 segments are about three times as broad as long but later ones rapidly increase in length; the 20th setiger is about as long as broad, and the 30th is 4 times longer than broad.

The first two segments behind the mouth lack parapodia or setae. They are well marked and there is no possibility that this is really a single biannulate segment.

Setigers 1-7 (segments 3-9) bear two bundles of crenulate capillaries arising directly from the sides of the body (see Text-fig. 8 p). Minute postsetal papillae

are present behind the notosetae and neurosetae from setiger 4 to 7 and on one of the paratypes the notopodial papilla may be traced forwards to setiger 1. Thus the thorax consists of 2 apodous segments and 7 setigers.

The change from thorax to abdomen is marked by the appearance of a bilobed neuropodial projection on setiger 8 (segment 10), the movement of the neuropodium from a lateral to a dorso-lateral position and the gradual lengthening of the segments. The abdominal parapodia (Text-fig. 8 *q*) are very simple. The notopodium consists of a small digitiform postsetal lobe and the neuropodium a stout bilobed projection from which the setae arise. The first pair of gills were only found on setiger 20 of the holotype and on setiger 24 on one of the paratypes. A conical papilla representing the intermediate cirrus appeared two segments later. There was no sign of a ventral cirrus. Thus the whole of the thoracic region and the anterior abdominal segments lack gills.

All the setae are simple crenulate capillaries and no specialised setae were found. The thoracic setae (Text-fig. 8 *m*, *m'*) both in the notopodium and the neuropodium are more numerous than those of the abdomen and their blades are rather stouter and the crenulations better marked. The abdominal notosetae are rather shorter than those on the thorax but the neurosetae are twice as long. There are only 2-3 of them and they are very smooth. The crenulations if present at all must be very poorly marked.

When first examined it was thought that these specimens belonged to the genus *Haploscoloplos*, but the presence of two anterior achaetous segments shows that they belonged to the new subfamily *Protoariciinae* erected by Hartman, 1957. This contains three genera, *Orbiniella*, *Protoaricia* and *Proscoloplos*. *Orbiniella* lacks gills and parapodial projections; *Protoaricia* has uncini and subuluncini in some thoracic neuropodia; *Proscoloplos* has swan-shaped hooks in the abdominal neuropodia. Thus these South African specimens must be referred to a new genus for which the name *Scoloplella* is proposed. Holotype: B.M.(N.H.), Reg. No. 1963.1.91.

***Haploscoloplos* cf. *fragilis* (Verrill, 1873)**

Anthostoma fragile Verrill, 1873: 598.

Hoploscoloplos fragilis: Hartman, 1957: 271, pl. 25, figs. 1-3.

RECORDS. SCD 223 (2 + 1 juv.).

NOTES. The three specimens are incomplete and rather damaged. The thorax consists of 15-16 setigerous segments sharply marked off from the abdomen by the change in the neuropodia. The setae are crenulate capillaries in both rami throughout the body, there being no hooks in thoracic neuropodia. In the thorax all the notopodia have well developed postsetal lobes which are somewhat flattened. Anterior neuropodia have a similar postsetal lobe (or foot papilla) behind the middle of the setal fascicle but on the last two thoracic segments there are 3 postsetal lobes. These all continue into the abdomen, the superior one becoming a neuropodial lobe and the two inferior ones becoming ventral cirri. This condition persists for 4 or 5 segments and then one papilla disappears leaving only a single small cirrus below the bilobed neuropodium. The abdominal notopodium has a slender

tapered postsetal lobe. There is also an interramal cirrus which appears on the last thoracic segment and gradually decreases in size on later abdominal segments. Branchiae appear on setigers 14-15, i.e. the penultimate thoracic segment. They are well developed and larger than the abdominal notopodia.

The possession of an interramal cirrus and ventral cirri immediately distinguish these specimens from *H. kerguelensis*. They agree in the main with Hartman's description of *H. fragilis* but differ in the number of thoracic setigers (setiger 15-16 vs. 17-23) and the origin of the gills (setiger 14-15 vs. 17-21 or 30). More material is required to determine how variable these characters are.

Family SPIONIDAE

Polydora maculata sp. n.

(Text-fig. 9 a-d)

RECORDS. SCD 284 (7).

DESCRIPTION. The type material was dredged at station SCD 284 at 33° 01' S./27° 55' E. in 7 metres. The specimens were extracted from burrows in an old *Bullia laevissima* shell inhabited by a hermit crab. A complete specimen chosen as the holotype measures 20 mm. by 1.0 mm. for 130 segments. The body is flesh pink apart from the palps which are barred with black.

The prostomium (Text-fig. 9 a) is faintly bilobed anteriorly and continues back as a median ridge reaching setiger 2. There are 4 eyes. Between the bases of the palps the prostomial ridge bears two occipital tentacles, one behind the other. The peristome forms a broad support for the prostomium and bears a pair of stout barred palps, which if folded back, would reach setiger 10.

The first setiger is small and bears cirriform notopodial and neuropodial lobes. Neurosetae are present but no notosetae. The notopodial lobes on setigers 2 to 4 are well developed and larger than those on setiger 6 or later segments. The neuropodial lobes increase in size on the first three setigers, decrease on setiger 4 and from setiger 6 onwards become insignificant and more ventrally situated. Setiger 5 as usual is swollen but bears no parapodial projections. Branchiae (Text-fig. 9 b) start on setiger 7 and continue to the posterior end. They are broad strap-like lobes quite separate from the notopodial lobes and just meet their fellows on the mid-dorsal line. The pygidium is small and saucer-shaped.

As mentioned above, there are no notosetae on the first foot. Subsequent feet have winged capillaries in the notopodia and there are no specialised posterior notosetae. The anterior neurosetae are also winged capillaries. Bidentate hooded hooks (Text-fig. 9 d) appear in the neuropodium of setiger 9 and as they barely project above the surface they are difficult to see. At first there are about 8-10 in a row but the number decreases to 4 near the posterior end. The enlarged hooks of setiger 5 are arranged in a curved row centred dorsally. There are about 6 of them alternating with abraded winged capillaries similar to those in other feet. Each hook (Text-fig. 9 c) has a stout shaft which curves and flattens at the tip.

Worn hooks are plain and blunt but a young hook has a narrow marginal flange. There are certainly no accessory teeth. Neither is there any separate tuft of capillaries on setiger 5.

The two striking features of this species are the possession of two occipital tentacles and the late appearance of the neuropodial hooks on setiger 9. Apart from these peculiarities there is some resemblance to *P. antennata* where the hooks appear on setiger 8 and there is one occipital tentacle. However the gills of *P. antennata* do not persist to the posterior end and the special hooks of setiger 5 are in a double, horseshoe-shaped row. There are also some resemblances to *P. kempfi* Southern but again *P. kempfi* has fewer gills and fang-like setae among the enlarged hooks of setiger 5. Holotype: B.M.(N.H.), Reg. No. 1963.1.94.

***Prionospio malmgreni* Claparède, 1870**

Prionospio Malmgreni Claparède, 1870: 73; Fauvel, 1927: 61, fig. 21 a-e.

RECORDS. WCD 82 (1), 97 (7); SCD 214 (2 + 1 juv.).

NOTES. These specimens agree in detail with Fauvel's description. There are 2 pairs of eyes of which the posterior, dorsal pair are the larger. There are 4 pairs of gills on setigers 2 to 5 of which the 2nd and 3rd are short and smooth while the 1st and 4th are both longer and pennate. There is a well marked membraneous ridge across the dorsum of setiger 7 and there are no genital pockets between middle parapodia. Neuropodial hooks start on setiger 11 and notopodial hooks on setiger 36.

There has been considerable doubt about the presence of this species at the Cape but as the above characters show, the present record is quite definite.

***Prionospio steenstrupi* Malmgren, 1867**

Prionospio Steenstrupi Malmgren, 1867: 202; Fauvel 1927, p. 60, fig. 21 f-i.

P. malmgreni var. *dubia* Day, 1961: 489, fig. 3 j-n.

RECORDS. WCD 73 (1), 82 (1), 86 (1), 97 (1), 109 (35 + 8 juvs.), 112 (20 + 5 juvs.), 116 (2 juvs.), 118 (68 + 4 juvs.), 122 (19); FAL 390 (1); SCD 154 (1), 185 (1), 187 (3), 200 (3), 223 (4), 228 (1 + 3 juvs.), 232 (6), 236 (2), 275 (4).

NOTES. The additional specimens show that the eyes which are indistinct in juveniles are invisible in adults. The fourth pair of gills are pennate and in South African specimens always shorter than the first pair. These features as well as the later appearance of neuropodial hooks and the lack of a membraneous ridge across setiger 7 distinguish this species from *P. malmgreni*.

***Prionospio* sp.**

RECORDS. SCD 223 (2 juvs.).

NOTES. The larger of the two specimens measured 4 mm. and is obviously a juvenile. However it certainly does not belong to any species recorded from South Africa.

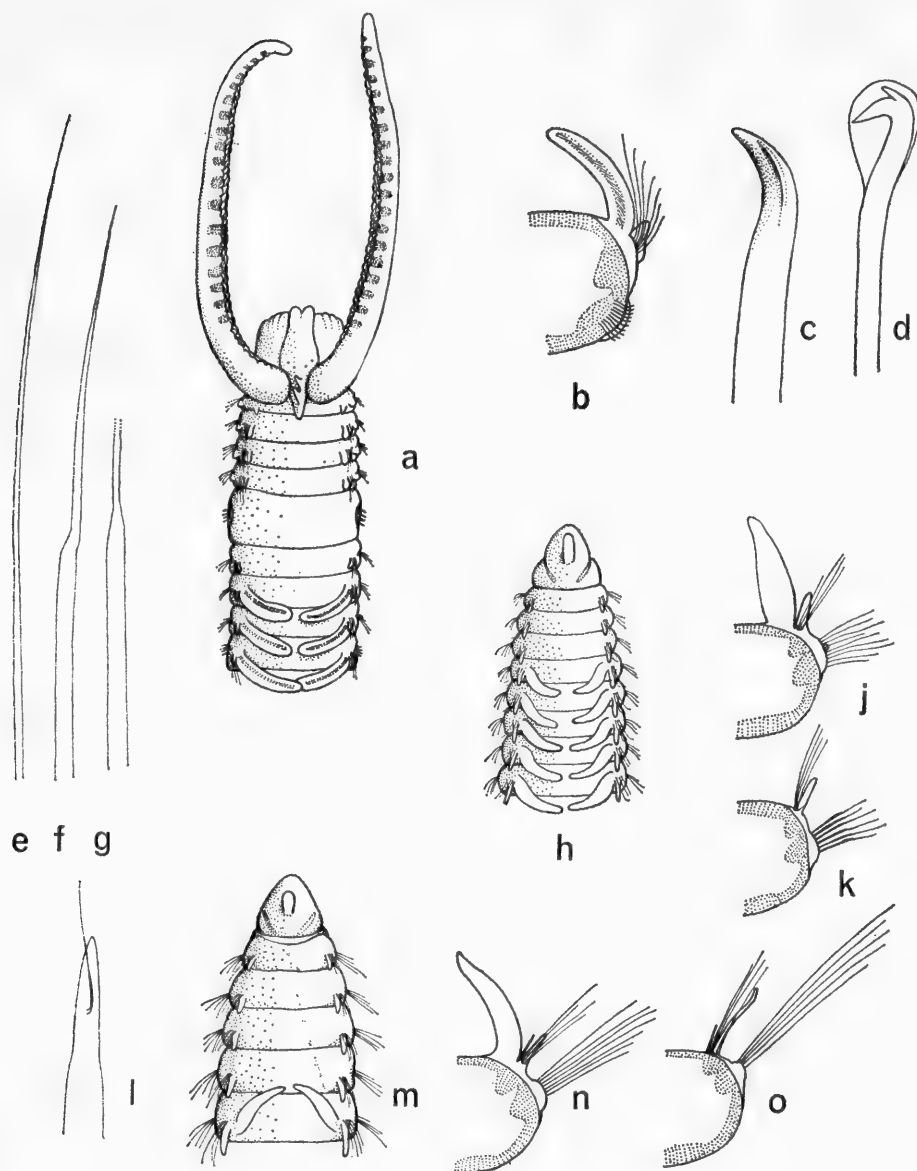


FIG. 9. *Polydora maculata*: (a) anterior end; (b) 11th foot; (c) enlarged hook from 5th foot; (d) neuropodial hook from 11th foot. *Aricidea curviseta*: (e) notopodial capillary from posterior foot; (f) lateral view of posterior neuroseta; (g) plan view of part of posterior neuroseta; (h) anterior end; (j) 20th foot and gill; (k) posterior foot. *Cirrophorus branchiatus*: (l) notopodial spine; (m) anterior end; (n) 16th foot; (o) 10th foot.

The prostomium is oval or shovel-shaped anteriorly and produced back as a ridge which reaches setiger 2. There are 2 pairs of eyes. The peristome lacks winglike expansions and the first setiger is small and without gills. Very long slender branchiae are present on setigers 2-10. Each gill is a smooth, cylindrical filament about 4 times as long as the segmental breadth though the last few are shorter. The postsetal lobes of the notopodia are never conspicuous; in the branchial region they are shorter than the notosetae and further back they are minute papillae no larger than the neuropodial lobes. Dorsal crests were not seen. Neuropodial hooks are certainly present on setiger 15 but possibly appear earlier.

These juveniles do not belong either to *P. cirrifera* or to *P. cirrobranchiata* the only species with approximately the same number of smooth gills. They might be juveniles of *P. polybranchia* Fauvel, 1929 which occurs in the tropical Indian Ocean and has over 40 pairs of gills in the adult.

Family PARAONIDAE

REMARKS ON THE FAMILY. Until recently only three species had been reported from South Africa, namely *Cirrophorus branchiatus* Ehlers, *Paraonis gracilis* (Tauber) and *Paraonis* (*Paraonides*) *lyra capensis* Day. Kirkegaard (1959) reported *Aricidea fauveli* Hartman and Day, 1961 added two new species namely *Aricidea capensis* and *Aricidea longobranchiata*. More recent collections include most of these and several new records. These are *Aricidea* (*Aedicira*) *belgicae* (Fauvel), *Aricidea curviseta* sp. n., *Aricidea jeffreysii* (McIntosh), *Aricidea suecica simplex* subsp. n., *Paraonis gracilis oculata* Hartman and *Paraonis* (*Paraonides*) *lyra lyra* Southern.

The identification of this material necessitated a review of generic characters. Useful reviews of the family are to be found in Cerruti (1909) and Hartman (1957).

The shape of the head is reasonably constant but there is some doubt about the buccal segment. According to Hartman "the first or second visible segment has biramous parapodia". Careful examination of the head shows that in *Aricidea* the mouth opens on the ventral surface of the head and there are faint grooves indicating that the head is formed of a dorsal prostomium with the achaetous peristomium reduced and fused to its ventral surface. A complete and well preserved specimen of *Cirrophorus branchiatus* Ehlers shows that the peristomium is not always so reduced. In this species a dorsal fillet of the peristome is visible between the prostomium and first setiger and the ventral part of the peristome is separated by a groove from the prostomium. In *Paraonis* the mouth is further back and the ventral surface of the first setiger forms the posterior lip. In brief, the first or buccal segment is reduced, always achaetous and fused to the ventral surface of the prostomium; the second segment is normally developed and bears the first pair of parapodia.

Hartman (1957) recognised two genera based on the presence or absence of a dorsal antenna and several subgenera based on the distribution of specialised setae. These characters are clear-cut and easy to observe and as the whole family includes some fifty species it is suggested that the subgenera be given full generic rank. The following key covers the species recorded from South Africa and one or two others marked with an asterisk which may be found in this area at a later date.

KEY TO GENERA AND SPECIES OF PARAONIDAE FROM SOUTH AFRICA

1. Prostomium with a median dorsal antenna 2
 Prostomium without an antenna 10
2. Specialised setae appear among the capillaries of posterior neuropodia (genus *Aricidea*) 3
 Specialised setae appear among the capillaries of posterior notopodia (genus *Cirro-phorus*) ***Cirrophorus branchiatus***
 No specialised setae among the capillaries either in the notopodia or neuropodia (genus *Aedicira*) ***Aedicira belgicae***
3. Specialised posterior neurosetae numerous with a stout shaft abruptly tapered to a slender blade 4
 Specialised posterior neurosetae as a few (5 or less) sigmoid hooks often with a hood 5
4. Specialised neurosetae with an incomplete joint at the junction of shaft and slender tip ***Aricidea fragilis****
 Specialised neurosetae with a kink but no joint at the junction of shaft and blade ***Aricidea curviseta***
5. Specialised neurosetae are sigmoid acicular hooks sometimes with a terminal filament but no hood 6
 Specialised neurosetae are hooks with a short or tapering hood over the apex 7
6. Acicular hooks with a terminal filament in middle segments but quite plain posteriorly
 Eyes present ***Aricidea suecica suecica****
 Acicular hooks without a terminal filament even in middle segments. No eyes ***Aricidea suecica simplex***
7. Specialised neurosetae with a rounded spioniform hood covering the blunt apex ***Aricidea jeffreysii***
 Specialised neurosetae with a delicate pointed hood or arista near the apex 8
8. Pointed hood or arista on the convex side of the apex. Posterior branchiae longer and stouter than middle ones ***Aricidea fauveli***
 Pointed hood or arista on the concave side of the apex 9
9. Last few branchiae with swollen bases and greatly elongated tips ***Aricidea longobranchiata***
 Last few branchiae decrease in size ***Aricidea capensis***
10. Specialised setae among the capillaries of posterior notopodia (genus *Paraonides*) 11
 Specialised setae among the capillaries of posterior neuropodia (genus *Paraonis*) 13
11. Modified notosetae are short, stout, broad-winged capillaries ***Paraonides neapolitana****
 Modified notsetae are forked setae 12
12. Postsetal lobe of anterior notopodia one-third the length of the branchia. Prostomium as broad as long ***Paraonidea lyra lyra***
 Postsetal lobe of anterior notopodia are minute, inconspicuous papillae. Prostomium longer than broad ***Paraonides lyra capensis***
13. Specialised neurosetae have a blunt, curved apex with a ventral guard. Branchiae foliaceous ***Paraonis fulgens****
 Specialised neurosetae are unidentate acicular hooks without hoods. Branchiae cirri-form 14
14. Prostomium with eyes ***Paraonis gracilis oculata***
 Prostomium without eyes ***Paraonis gracilis gracilis***

Aricidea curviseta sp. n.

(Text-fig. 9 e-k)

SCD 197 (1), 237 (3).

DESCRIPTION. The type material comes from station SCD 237. The holotype is 16 mm. long by 0.7 mm. across the branchial region but the posterior region is more slender and rounded. There are 83 segments but the tail end is missing.

The prostomium (Text-fig. 9 h) overlies the small achaetous peristomium and is fused to it though lateral grooves remain. The whole forms a bluntly triangular head about as broad as long. There are no eyes and the median antenna does not reach the tip of the prostomium. The first few setigers are narrowed but in the branchial region each segment is about four times as broad as long. Branchiae appear on segment 4 and persist to segment 40. In other specimens as many as 40 pairs of gills have been observed. Each gill (Text-fig. 9 j) is a stout tapered projection which just meets its fellow in the mid-dorsal line. The last few decrease gradually in size and there is no posterior groups of elongate branchiae. The postsetal lobe of the notopodium is evident from the first segment and is at first rather short and conical. It soon becomes more slender and in the branchial region it is a little less than a third the length of the branchia. There is a small postsetal neuropodial papilla behind the slight lateral swelling on which the seta arise in the branchial region.

In the posterior region the segments are longer, hardly twice as broad as long. The postsetal lobe of the notopodium (Text-fig. 9 k) is a slender filament no longer than that in the branchial region and only half the length of the notosetae. There is no neuropodial projection.

There are two types of setae. In the branchial region both the notosetae and the neurosetae are tapered capillaries without obvious blades or marked curvature. In the posterior notopodia the capillaries (Text-fig. 9 e) are more slender and the number of setae is reduced. Posterior neurosetae (Text-fig. 9 f and g) however are quite different. All neurosetae are similar throughout the posterior region and each consists of a stout shaft which suddenly narrows to a long slender tip. When seen in surface view (Text-fig. 9 g) the sudden narrowing is the only obvious feature but when seen in lateral view (Text-fig. 9 f) it is evident that there is an abrupt curve or kink at the origin of the slender tip. There is no hood or projecting tooth at the point of curvature but the kink forms a slight step and the tip may break off leaving only the stout shaft.

Possibly this species is most closely related to *A. uschakovi* Zachs, 1925 from Arctic seas or possibly to *A. fragilis* Webster, 1879 from Sweden. In the former each posterior neuroseta has a fine hairlike arista at the end of the stout sigmoid shaft, which might be a further development of the abrupt decrease in thickness which occurs in *A. curviseta*.

In *A. fragilis* as described by Hartman (1957) there is an incomplete joint or pseudoarticulation at the junction of the stout shaft and the slender blade. There is no sign of such an articulation in *A. curviseta*. Holotype: B.M.(N.H.), Reg. No. 1963.1.106.

Aricidea jeffreysii (McIntosh, 1879) *sensu* Cerruti, 1909

Scolecolepis Jeffreysii McIntosh, 1879 : 506, pl. 65, figs. 13, 14.

Aricidea jeffreysii : Cerruti, 1909 : 409, pl. 18, figs. 1-6, 9-18, 22-26 ; Fauvel, 1927 : 75, fig. 25 a-e.

RECORDS. FAL 397 (1).

NOTES. The single specimen is incomplete, measuring 9 mm. by 0.4 mm. for 70 segments. The prostomium is bluntly rounded anteriorly and lacks eye-spots. The median antenna is cylindrical and just projects beyond the anterior margin of the prostomium. Branchiae start on setiger 4 and extend over 18 segments. Each is bluntly cylindrical and its length equals half the width of the segment. The postsetal lobes of anterior segments are tapered and half as long as the gills ; in posterior segments they remain the same length but become very slender. Most of the setae are capillaries which are curved anteriorly but fine and straight posteriorly. The specialised neuropodial setae are 4-5 hooks which appear in the postbranchial region. The tip curves to a blunt apex which has a rounded spioniform hood.

This is a new record for South Africa but the above description agrees with the account given by Fauvel with three exceptions. The South African form lacks eye-spots, has a longer antennae and considerably shorter gills than shown by Fauvel's fig. 25 a.

Hartman (1957) reported that McIntosh's description of the holotype from Greenland is incomplete and that the description given by Cerruti (1909) and Fauvel (1927) may refer to a different species.

Cirrophorus branchiatus Ehlers, 1908

(Text-fig. 9 l-o)

Cirrophorus branchiatus Ehlers, 1908 : 124, pl. 17, figs. 5-9.

Aricidea (*Cirrophorus*) *branchiata* : Hartman, 1957 : 323.

RECORDS. WCD 82 (1).

NOTES. Ehlers' holotype from the Agulhas bank was incomplete and the present complete and well preserved specimen allows me to amend the original description of this rare species.

The complete worm measures 25 mm. by 0.4 mm. for 120 segments. The body is somewhat flattened with short anterior segments about 3-4 times as broad as long and longer posterior segments less than twice as broad as long. The intersegmental constrictions are very marked posteriorly so that this region appears almost moniliform.

The prostomium (Text-fig. 9 m) is a blunt depressed cone without eyes but has well-marked nuchal slits. The median antenna is short and stout, less than half the length of the prostomium. Ehlers, p. 17, fig. 6, shows the first segment as bearing setae but in fact there is a short peristomial segment between the prostomium and the first setiger. It is just visible dorsally but extends forward below the prostomium ventrally.

In the anterior region the postsetal lobes of the notopodia (Text-fig. 9 *n*) are well developed but in the middle of the body they are reduced until they are no longer than the notopodial spines and then in the posterior region (Text-fig. 9 *o*) they become very long and slender. At the very end of the body there are 4 pairs of cirriform projections. One pair certainly arises from the pygidium but the others may be the postsetal lobes of developing segments. The neuropodia are mere lateral swellings throughout the whole length of the body.

Branchiae appear on setiger 5 and continue for the next 23 segments. Each is a cylindro-conical organ arching forward over the back and its length is equal to $2/3$ the segmental breadth. The last 2-3 pairs are shorter.

Anterior setae up to segment 12 are all fine capillaries without a trace of a blade. From setiger 13 however, 1-2 heavy spines appear in the notopodia and the notopodial capillaries are reduced in number from over 20 in anterior segments to about 6 in posterior ones. Each spine (Text-fig. 9 *l*) is straight and pointed with a very fine curved filament arising some distance below the pointed apex. These filaments were not noted by Ehlers and are easily mistaken for developing capillaries but the examination of several parapodia shows that they occur on all spines that are unbroken. No specialised setae appear in the neuropodia but the capillaries increase in length until they are longer than the segmental breadth and twice as long as the notosetae.

Aedicira belgicae (Fauvel, 1936)

Paraonis Belgicae Fauvel, 1936 : 29.

Aricidea belgicae : Monro, 1939 : 127, fig. 16 *a-b*.

Aricidea (Aedicira) belgicae : Hartman, 1957 : 327.

RECORDS. WCD 109 (3).

NOTES. *Aedicira* was erected by Hartman (1957) as a subgenus of *Aricidea* which lacked specialised neurosetae in posterior parapodia. The type species is *Aricidea (Aedicira) pacifica* Hartman, 1944. As explained earlier, *Aedicira* is here recognised as a full genus characterised by the possession of a median antenna and the lack of specialised setae either in the notopodia or neuropodia.

The three specimens are all incomplete. The longest is 18 mm. by 0.9 mm. for 84 segments. The prostomium which is broadly rounded anteriorly agrees very well with Monro's figure. The peristome is not visible dorsally but may be distinguished ventrally where it is largely fused to the prostomium.

The anterior region is rather flattened with segments 6 times as broad as long ; the posterior region however is more rounded with segments only twice as broad as long. Branchiae appear on setiger 4 and extend over 24 segments. An average gill is a stout tapered organ whose length is equal to $2/3$ the breadth of the segment. The last few gills however are markedly swollen basally and then taper abruptly to short filamentous tips. The postsetal lobe of the notopodium is well developed and tapered and on branchial segments it is half the length of the gill. Posteriorly it becomes very slender but remains the same length.

The capillary setae of both rami in the anterior region are numerous and curved. In the postbranchial region the number of setae decrease particularly in the noto-

podium where only a few fine capillaries remain. The neurosetae are also fine and about as long as the segment is broad. There are no modified setae in either ramus.

Aedicira belgicae is an Antarctic species and has not been recorded from South Africa before. The genus is characterised by the lack of specialised setae and as the specimen is broken at segment 84 some doubt as to the identification must remain.

***Paraonis gracilis gracilis* (Tauber, 1879)**

Aonides gracilis Tauber, 1879 : 115.

Paraonis gracilis : Hartman, 1957 : 330, pl. 44, figs. 4-5.

Aonides gracilis : Ehlers, 1913, p. 512.

RECORDS. SCD 223 (7).

NOTES. The only other record of this species from South Africa is Ehlers' doubtful record from False Bay ("Simonstown"). In Ehlers' brief description there is no mention of eyes, a character which separates *P. gracilis gracilis* from *P. gracilis oculata* Hartman, 1957, a subspecies which has recently been recorded by me (Day, 1963) from 1200 metres west of Cape Town.

The present specimens agree in detail with the stem form. They lack eyes and there are about 12 pairs of branchiae starting on setiger 7-9. The postsetal notopodial lobes are small throughout and the specialised neurosetae of the posterior region are 2-3 stout sigmoid hooks with blunt unidentate tips and no trace of a hood or arista.

This species seems to be world wide in distribution.

***Paraonides lyra lyra* (Southern, 1914)**

Paraonis (Paraonides) lyra Southern, 1914 : 94, pls. 9-10, fig. 22 a-c ; Fauvel, 1927 : 72, fig. 24 a-f.

RECORDS. WCD 112 (common).

NOTES. *Paraonides lyra capensis* (Day, 1955) was reported by me as *Paraonis lyra* var. *capensis* from the Knysna estuary. When the present specimens were compared with paratypes of *P. l. capensis* the following differences were observed.

In *P. l. capensis* the prostomium is obviously longer than broad, the postsetal lobes are always minute or invisible and the setae are shorter than the width of the body. In *P. l. lyra* the prostomium is about as broad as long, the postsetal lobes of the notopodia are well marked in the branchial region and in the posterior region the neuropodial capillaries are much longer than the segmental width. Southern has suggested that the latter character may be a sexual feature.

? *Paraonides* sp.

RECORDS. WCD 92 (2).

NOTES. Two minute threadlike worms 4 mm. long by 0.1 mm. but broken after the 46th setiger. At first sight there appear to be no projections of any sort.

Examination under high power shows an ovoid prostomium without an antenna but with a pair of minute eyes, a reduced achaetous peristome quite separate from the prostomium and behind this numerous biramous segments. The notopodia bear minute postsetal papillae which are easily overlooked and there are no gills. There are no neuropodial projections. There are slender capillaries in both rami throughout the body and in addition there are 1-2 short forked setae in the notopodia from setiger 2. These are similar to the forked setae of *Paraonides lyra* with the longer ramus bearing spinules on its inner margin.

The absence of gills is peculiar. It is possible however that they are juveniles and that gills develop later.

Family COSSURIDAE nov.

REMARKS. The family Cirratulidae to which the genus *Cossura* Webster & Benedict, 1887 has hitherto been referred, has been a dumping ground for a wide diversity of genera. Fauvel (1927) recognised 12 European genera divided between two subfamilies. Hartman (1959) agreed with earlier workers in transferring *Streblospio* to the Spionidae and recognised *Ctenodrilidae* Kennel, 1882 as distinct from *Cirratulidae* Carus, 1862. Within the Cirratulidae she recognised 14 valid genera. Among these are *Acrocirrus*, *Ledon* and *Macrochaeta* all of which have prostomial projections and compound setae and *Caulleriella*, *Chaetozone*, *Cirratulispio*, *Cirratulus*, *Cirriformia*, *Cossura*, *Dodecaceria*, *Pentacirrus*, *Pseudocirratulus*, *Tharyx* and *Timarete* which lack prostomial projections and have no compound setae.

The genus *Cossura* is now known through 5 species. It agrees with the typical cirratulids in lacking prostomial projections and projecting parapodia and in possessing capillary setae with flattened blades. However it differs from typical cirratulid genera in three important features. It lacks grooved food-gathering peristomial palps or the homologous grooved tentacles inserted on anterior segments. It lacks paired cylindrical gills above the notosetae and it possesses 3 long anal cirri. The only projection is a single very long median gill which arises from the second or third setigerous segment. Some workers have referred to this as a "tentacle" but it is quite different in structure from the grooved tentacles of the typical cirratulids.

There is no more reason to include *Cossura* among the Cirratulidae than there is to include *Paraonis* which does possess gills. It is suggested in fact that *Cossura* should be placed in a new family, *Cossuridae*, defined as follows:

Small threadlike worms with numerous similar segments. Prostomium conical. Pharynx eversible, soft and unarmed. No head appendages either on the prostomium or peristomium. No parapodial lobes on any segment. The first 1-2 segments behind the peristomium achaetous but subsequent segments with one or two bundles of simple capillary setae which usually have flattened blades with spinulose margins. A single very long branchial filament arises from the middle of the dorsum of setiger 2 or 3. Pygidium often with 3 long anal cirri.

Cossura coasta Kitamori, 1960

Cossura coasta Kitamori, 1960 : 1082, fig. 1 a-f.

RECORDS. WCD 53 (1 juv.), 79 (1), 106 (12) ; SCD 228 (3), 232 (1).

NOTES. The prostomium is a blunt cone a little longer than broad. There are no eyes nor head appendages. Behind the prostomium there are two apodous rings with the ventral mouth opening between them. Each of the rings is as long as one of the setigerous segments. They are regarded here as the peristome and the second segment but it is possible that the first ring is part of a biannulated prostomium or that the two rings together form part of a biannulate peristome. The proboscis which was everted on one specimen has a lobed margin.

Behind the second apodous ring there are 40 cylindrical setigerous segments in the longest fragment which measures 7 mm ; none of the specimens was complete.

There are no parapodial projections and the setae arise directly from the sides of the body. In the posterior segments the setae obviously arise in two fans, so that these segments are clearly biramous. Further forward however the two bundles approach one another very closely, until those of the first setiger form a single bundle. The second and subsequent setigers seem to have two bundles but some doubt must remain. In each ramus the setae are arranged in two rows ; an anterior row of shorter setae and a posterior row of longer ones, almost twice the length of the anterior row. All setae are capillaries with rather flattened blades having a spinulose or hispid margin.

A single very long slender gill (the "tentacle" of other workers) arises from the anterior margin of setiger 3 in the mid-dorsal line. In contracted specimens it is not very clear whether this gill actually arises from setiger 3 or setiger 2.

A discussion of the species of *Cossura* is given by Reish (1958). The specific differences are based on the number of apodous segments behind the prostomium, the number of uniramous setigerous segments and the position of the gill. As shown above these differences are somewhat slender evidence for specific identification but the characters of the present specimens fit the description of *C. coasta* Kitamori from Japan better than others. *C. coasta* however is very close to *C. candida* Hartman (1955) from California.

As far as I am aware this is the first record of *Cossura* from the Southern hemisphere.

Family CIRRATULIDAE

Tharyx marioni (St. Joseph, 1894)

Heterocirrus Marioni Saint-Joseph, 1894 : 56.

Tharyx marioni : Fauvel, 1927 : 100, fig. 35 a-b ; Day, 1961 : 503 with synonymy.

RECORDS. One specimen obtained by a dredger prospecting for diamonds north of the Orange River mouth in 5-10 fathoms.

NOTES. This is a new record for South West Africa.

Family OPHELIIDAE

Ophelia cf. *roscoffensis* Augener, 1910

Ophelia roscoffensis Augener, 1910 : 237.

RECORDS. SCD 247 (1 + 1 juv.).

NOTES. The larger of the two specimens is 18 mm. long. It has the usual fusiform shape with 8 prebranchial, 20-21 branchial and 3-4 posterior abbranchiate segments, there being one more gill on one side. Thus the total is 32 setigers. There is no achaetous segment before the pygidium. Branchial fenestrations are absent.

Crimped dorso-lateral ridges extend from setiger 29 to the pygidium which bears an arc of 12 small cirri dorsally and two very stout conical cirri ventrally. The neurosetae are half the length of the notosetae and the gills taper evenly.

O. roscoffensis was redescribed by Tebble (1952 : 565, fig. 5) from a large (51 mm.) specimen obtained off Plymouth ; it has 8 abbranchiate, 23 branchiate and 1 posterior abbranchiate setiger making a total of 32 setigers as in the present specimens. However it has 2-3 more branchial segments and correspondingly fewer posterior abbranchiate setigers. It may be that additional branchiae appear on larger individuals. It also agrees in the lack of branchial fenestrations and in the details of the pygidium. *Ophelia praetiosa* (Kinberg) from Patagonia as described by Hartman (1948 : 115) is also close with 8 abbranchiate, 18 branchiate and 5 postbranchial setigers making a total of 31 setigers. This species also lacks branchial fenestrations but has 19 small anal cirri as well as the large ventral pair.

More material is required to determine the variability in numbers of branchiae.

Family SCALIBREGMIDAE

Asclerocheilus capensis sp. n.

(Text-fig. 10 a-f)

RECORDS. SCD 236 (1).

DESCRIPTION. The type locality is 34° 51' S./23° 41' E. in 183 metres. The holotype is a single incomplete specimen 5 mm. long by 1.0 mm. broad with 16 setigers and probably represents half of the complete worm.

The prostomium (Text-fig. 10 a) is quite pale without any trace of eye-spots and bears a pair of short stout lateral lobes. The peristome is achaetous, narrow dorsally and incomplete ventrally so that the lower lip appears to be formed by setiger 1.

The body is oval in section and somewhat depressed with the first 10 to 12 setigers broader than those which follow. The first three setigers are not clearly annulated but from the 6th onward all segments are quadriannulate and tessellated dorsally. The ventral marks are not so regular or clearly defined. There are no parapodial lobes or gills and the setae arise from slight swellings on the body wall. Anterior notosetae are dorsal in origin but later ones from about the 12th segment are lateral like the neurosetae.

Setigers 1 and 2 bear curved acicular setae and capillaries in both rami. There are 15 or more curved acicular setae in the notopodium of setiger 1 and 4-6 long capillaries, but in the neuropodium there are only a few acicular setae, many more capillaries, and the distinction between the two types of setae is not so marked. In setiger 2 (Text-fig. 10 *b*) the notopodium has only about 6 acicular setae and an equal number of capillaries. All subsequent segments (Text-fig. 10 *c*) lack acicular setae and bear long fine capillaries and a few short forked setae in both rami.

The capillaries (Text-fig. 10 *f*) are fine and tapered without any ornamentation. The acicular setae (Text-fig. 10 *e*) are fairly stout and taper abruptly near the end to fine tips. The forked setae (Text-fig. 10 *d*) have two unequal prongs and the inner margins of both are spinulose.

Two species of the genus *Asclerocheilus* have been described, namely *A. intermedius* (St. J.) with acicular setae in both rami of setigers 1, 2 and 3, and *A. beringianus* Uschakov, 1955 from the Bering Sea with acicular setae confined to the notopodia of setigers 1 and 2. *A. capensis* appears to be intermediate between the two, but further work may show that all three are merely growth forms of *A. intermedius*. Holotype: B.M.(N.H.), Reg. No. 1963.1.132.

Parasclerocheilus capensis Day, 1961

Parasclerocheilus capensis Day, 1961: 517, fig. 10 *c-f*.

RECORDS. Collected by a dredger prospecting for diamonds in 10-20 metres just north of the Orange River mouth.

NOTES. This is a new record for South West Africa.

Family MALDANIDAE

Euchymene sp.

(Text-fig. 10 *g*)

RECORDS. SCD 187 (fragments).

NOTES. Although the material contains both anterior and posterior ends, the number of setigers is unknown. Nevertheless the characters suggest that the species is new to South Africa and thus worth recording.

The prostomium is bluntly triangular but lacks ocelli. The cephalic plate is oval with a well developed rim which slopes back smoothly to a median posterior notch. There are no lateral notches. The nuchal grooves are long and straight, fully $\frac{4}{5}$ the length of the cephalic plate.

Setigers 1-5 are short but 6 and 7 are longer. Setiger 8 is shorter than 7 but subsequent ones become 4-5 times longer than broad. Glandular bands are well marked from setiger 3 to 6, and there is a faint midventral streak from setiger 1 onwards. The posterior end bears two achaetous preanal segments in front of the well marked pygidial ring and funnel. The two preanals together are just shorter than the last setiger and the first is twice as long as the second. The funnel has 18-24 cirri which alternate in length; the ventral one is much longer than the rest. The anus is sunk in the funnel and a ventral valve is lacking.

Notosetae include the usual winged capillaries with a few fine feathered forms in posterior notopodia. The neurosetae of setigers 1-3 are represented by 2-3 acicular spines (Text-fig. 10 g) with sharply bent ends bearing 3 vestigial denticles above the rostrum but no trace of a tendon below. Later neurosetae are numerous well developed hooks with a vertical series of 6-7 teeth above the main fang and strong tendons below.

The only species of *Euclymene* recorded from South Africa with a smooth (non-crenulate) cephalic margin and 2-3 acicular neurosetae with denticles is *E. oerstedii*. Kirkegaard's (1959) record from the Cape is based on a fragmentary specimen and thus doubtful. The present material however has only two achaetous preanals, no ocelli and lacks lateral notches in the cephalic margin.

***Euclymene* cf. *quadrilobata* (Sars, 1865)**

(Text-fig. 10 h-j)

Clymene quadrilobata Sars, 1865 : 15.

RECORDS. SCD 223 (3 fragmentary specimens).

NOTES. The specimens are all broken. The longest fragment has 13 setigers and measures 45 mm. by 1.0 mm. The fragments obviously belong to a species new to South Africa but the number of setigerous segments is unknown. The main characters may be summarised as follows :

Anterior end truncate with a rounded cephalic plate (Text-fig. 10 h) almost at right angles to the body. Prostomium small and rounded. Eye-spots present. Nuchal grooves straight, very short, less than half the length of the cephalic plate. Cephalic rim very low and thick with a pair of lateral depressions and a single median posterior notch. Number of setigerous segments unknown. Glandular bands well marked on setigers 3 to 7. A faint mid-ventral streak from setiger 1 onwards. Posterior end with 4 achaetous preanals each half as long as the last setiger. Pygidial ring and funnel well marked, the latter bearing 24 unequal cirri. Anus sunken in the funnel. No ventral valve. Notosetae are winged capillaries. Neurosetae of setigers 1-3 represented by a single stout spine (Text-fig. 10 j) with faint indications of denticles above the rostrum. Later neurosetae are rows of numerous hooks each with 4-5 well developed teeth above the main fang and a few fine tendons below.

The main characters are generally similar to those described by Arwidsson (1906) for *Pseudoclymene quadrilobata* (Sars) and there are also resemblances to *Clymene* (*Isocirrus*) *wolffi* Kirkegaard, 1959 from the Gold Coast.

***Praxillella* cf. *affinis* (Sars, 1872)**

(Text-fig. 10 k-l)

Clymene affinis Sars, 1872 : 412.

Clymene (*Praxillella*) *affinis* : Fauvel, 1927 : 180, fig. 62 f-l.

RECORDS. WCD 112 (2).

NOTES. The largest of the two specimens was complete and measured 23 mm.

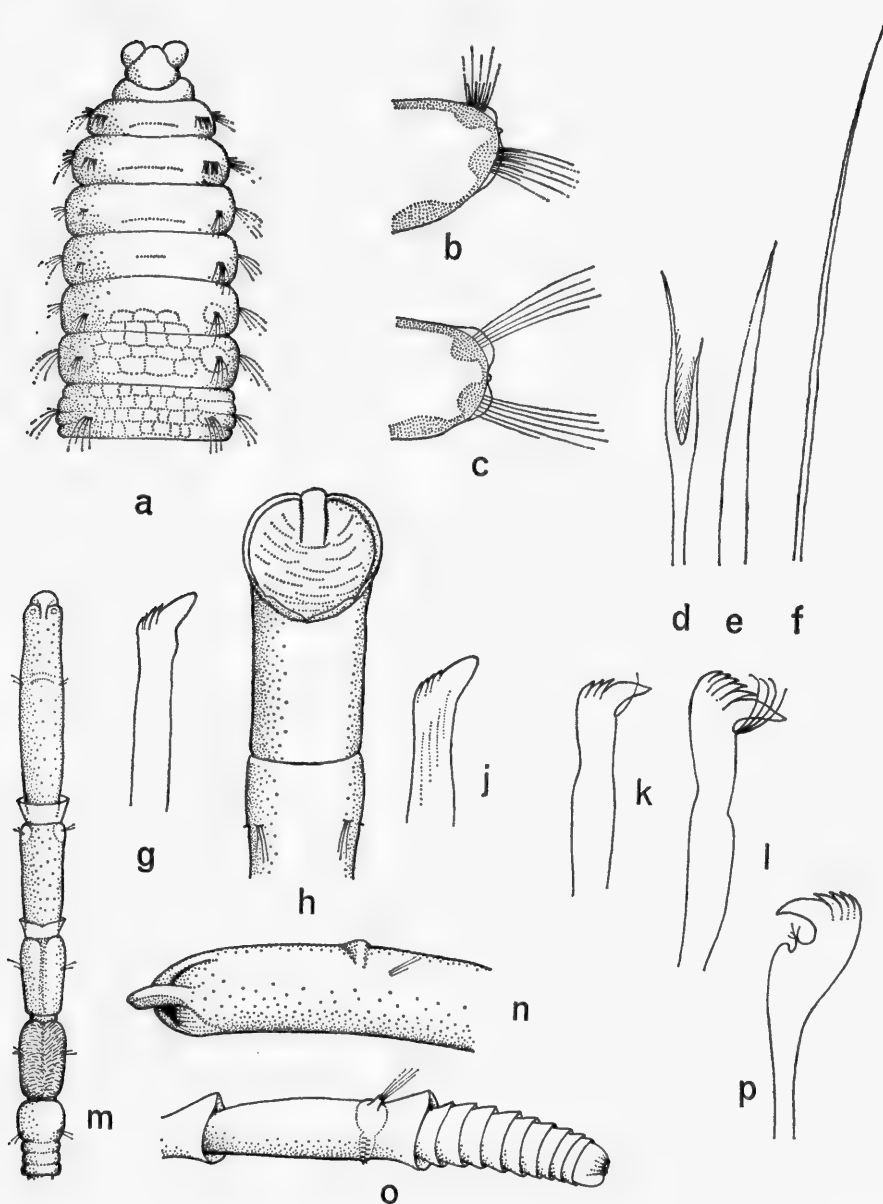


FIG. 10. *Asclerocheilus capensis*: (a) anterior end; (b) 2nd foot; (c) 12th foot; (d) forked seta; (e) notopodial acicular seta from 2nd foot; (f) capillary seta. *Euclymene* cf. *oerstedii*: (g) neuropodial spine from 2nd foot *Euclymene* cf. *quadrilobata*: (h) head; (j) neuropodial spine from 2nd foot. *Praxillella* cf. *affinis*: (k) neuropodial spine of 2nd foot; (l) neuropodial hook from 5th foot. *Rhodine gracilior*: (m) dorsal view of anterior end; (n) lateral view of head; (o) lateral view of posterior end; (p) neuropodial hook.

by 0.4 mm. It is uniformly pale brown in alcohol. There are 18 setigerous segments, 3 achaetous preanals followed by the pygidium which has a circle of 12 subequal cirri and a protruding anal cone with a large ventral valve.

The prostomium is bluntly triangular without eyespots. The cephalic plate is oval and the marginal rim has a pair of faint lateral notches and a better marked posterior notch. The rim is high in front of the lateral notches and distinctly lower behind them. The nuchal grooves are long and straight, fully $\frac{4}{5}$ the length of the cephalic plate. Setigers 1-8 are 2 to 3 times longer than broad, setigers 9-15 about 4 times as long as broad, but later ones gradually shorten until the 3 preanals are together just equal to the length of the last two setigers. Setiger 1-3 have slight anterior glandular bands, setigers 4-8 are markedly glandular and from setiger 8 onwards there is a narrow mid-ventral glandular streak.

Setiger 1-3 have 2-3 hooks in each neuropodium but each of the later segments has a row of about 10. The hooks of the first three setigers (Text-fig. 10 *k*) have 3 well marked teeth above the rostrum and there is even a trace of a tendon below. The hooks of later setigers (Text-fig. 10 *l*) are much better developed with a vertical crest of about 5 denticles above the rostrum and well marked tendons below. The notosetae include about 4 stout capillaries with narrow wings and 3 fine capillaries without visible wings.

There are several differences between the South African form described above and Fauvel's account of *P. affinis*. Eye-spots are absent, there is no enlarged anal cirrus, the finer notosetae are not spinulose and above all the neurosetae of setigers 1-3 have much better developed denticles and even possess faint tendons, so that the anterior neurosetae approach the condition found in the genus *Axiiothella*. However, these South African specimens are small and these may be juvenile characters. Some doubt as to the identification must remain until larger specimens have been found.

As shown earlier (Day, 1955), *Praxilla capensis* McIntosh, 1885 is indeterminate since the posterior end is missing. In any case the neurosetae of setiger 1-3 are smooth, straight and acicular, one per parapodium.

Lumbriclymene cylindricauda Sars, 1872

Lumbriclymene cylindricauda Sars, 1872 : 413 ; Arwidsson, 1906 : 40, pl. 1, figs. 15-24 ; pl. 7, figs. 219-221.

RECORDS. SCD 237 (1 juv.), 251 (1).

NOTES. The adult specimen is broken into two pieces which together measure 60 mm. by 1 mm. while the juvenile was complete with 19 setigers and measured 35 mm. There are 3 well developed achaetous preanals and then 3 indefinite ones preceding the bluntly conical pygidium.

These specimens agree with Arwidsson's description with one or two minor exceptions. The colour markings appear to differ. There is a dorsal brown bar on the buccal segment and similar bars in front of and behind each parapodium of the first three setigers ; there is also a well marked midventral glandular streak stretching

from setiger 11 to setiger 14, and the neuropodial hooks on setiger 4 have 4 teeth above the main fang, not 2-3. Later hooks also have 4, but there are minor lateral teeth as well.

The juvenile was encased in a brittle tube composed of coarse sand and foraminiferan shells.

The only other species of the genus recorded from South Africa is *L. minor* which differs in having only 3 achaetous preanals and a dorsal anus.

***Rhodine gracilior* Tauber, 1879**

(Text-fig. 10 *m-p*)

Rhodine loveni gracilior Tauber, 1879 : 123.

Rhodine gracilior : Arwidsson, 1906 : 74, pl. 2, figs. 53-58 ; pl. 7, figs. 237-241 ; pl. 8, figs. 242-243 ; Wesenberg-Lund, 1949 : 344 ; Kirkegaard, 1959 : 65.

Rhodine cf. *gracilior* : Day, 1961 : 514.

RECORDS. WCD 86 (3), 112 (2), 118 (2), 121 (1).

NOTES. The additional material includes an anterior fragment with a head and 13 setigers (Text-fig. 10 *m*), a posterior fragment with 7 setigers, 10 achaetous preanals and the pygidium and finally a juvenile with 21 setigers but without a head or posterior end. It is estimated that an adult was about 50 mm. long by 1 mm. wide with a minimum of 23 setigers.

The striking features include the very long head and first setiger (Text-fig. 10 *n*), the dark red 4th setiger, the smooth-edged posterior collars on posterior segments, (Text-fig. 10 *o*) the numerous achaetous preanals, the bluntly conical pygidium and the backwardly bent and expanded heads of the hooks (Text-fig. 10 *p*).

The tube is fragile and membranous.

Family PECTINARIIDAE

***Pectinaria capensis* (Pallas, 1766)**

Nereis cylindraria capensis Pallas, 1778 : 118.

Pectinaria capensis : McIntosh, 1904 : 76, pl. 7, figs. 35-36 ; Day 1955, p. 432.

RECORDS. In 10 metres on sand, 20 miles north of Orange River mouth.

NOTES. This species has not been recorded from South West Africa before. It was obtained by a suction dredger prospecting for diamonds. The specimens are large (up to 120 mm. long) and unusual in that the tube is composed of sand grains arranged in regular transverse rows. All Cape specimens examined have tubes composed of short lengths of sponge spicules arranged like bonded bricks. Careful comparison of the Cape and South West African forms showed no differences in the animal but the description given by me (Day, 1955) needs amendment.

There may be 11 or as many as 15 paleae on each side, there is one, not two achaetous prescapal segments and a slender anal cirrus is present on the ligule though often broken off. It may be added that the scaphe is oval in outline, and concave dorsally with 2 pairs of cirriform marginal papillae near the base and one pair distally near the origin of the ligule.

***Pectinaria (Lagis) koreni cirrata* subsp. n.**

(Text-fig. 11 a)

RECORDS. NAD 27 (2)—dredged on 13th July, 1959 off the Natal coast at 29° 53·5' S./31° 06·5' E. in 71 metres on dark brown sand.

DESCRIPTION. The holotype is 11 mm. long by 2 mm. across the first setiger. The tube is composed of coarse sand grains.

Operculum (Text-fig. 11 a) with 10 + 10 paleae. Margin of the operculum smooth and unusually high. Its ventral ends are fused to the bases of the first pair of tentacular cirri. The veil which bears about 18 slender marginal cirri is also fused to the bases of the tentacular cirri on each side so that the tentacular cirri mark the junction of the veil and opercular margin, i.e. the veil is completely fused to the operculum. First pair of tentacular cirri slender and longer than the paleae; second pair a little shorter. The semicircular ventral flange between the second pair of tentacular cirri is incised to form 15–20 slender cirri. Two pairs of lamellate gills. Ventrums of branchiferous segments and setiger 1–2 with three glandular ventral pads.

Behind the branchiferous segments there are 3 segments with notosetae only, 12 segments with notosetae and uncini, and then 2 achaetous prescapal segments followed by the scaphe.

The scaphe is oval and the margin is incised to form a median basal lappet and 5 pairs of marginal lappets. Scapal hooks were not seen but were probably retracted. The anal ligule is tongue-shaped with a smooth margin and a small anal cirrus.

Notosetae include a series of broad-bladed capillaries and a smaller series of capillaries with bent and finely dentate tips. Uncini have 2 rows of 5–6 large teeth and a close set group of numerous small teeth above the basal gouge.

The main characters are similar to those of *P. (Lagis) koreni* but the slender cirri on the ventral flange between the second pair of tentacular cirri are quite different from the 8–10 blunt lobes found on the same flange of *P. koreni*. Holotype: B.M.(N.H.), Reg. No. 1963.1.138.

Family AMPHARETIDAE***Isolda pulchella* Müller, 1858**

Isolda pulchella F. Müller, 1858: 219; Augener, 1918: 517, pl. 7, fig. 229, text fig. 88.

Isolda warnebroensis Augener, 1914: 82, pl. 1, figs. 14–15, text-figs. 13 a–c.

Isolda sibogai Caullery, 1944: 102, fig. 83.

MATERIAL EXAMINED. British Museum (Natural History) Reg. No. 76: 10: 4: 13 from Brasil *I. pulchella* (Müller det.) and Reg. No. 1933: 3: 18: 67–69 from Burma, *I. warnebroensis* (Monro det.).

S. A. RECORD. SCD 187 (2 + 1 juv.).

A comparison of the specimen of *I. pulchella* from Brasil, of *I. warnebroensis* from Burma and the large fresh specimens from South Africa shows that they are all

identical. Since there is no modern description of *I. pulchella* and some doubt as to its relations with other species, a short description is given below and the various species discussed.

Body up to 45 mm. long with 60 segments. Colour brown, buccal cirri speckled when fresh. Prostomium snoutlike, rounded anteriorly and pinched in at the sides. No eyes nor glandular ridges. Buccal cirri short, stout, without papillae but grooved along one side. Two swollen lateral folds along the sides of the head extend back to segment VI and join a transverse dorsal fold which has a smooth margin. Two groups of 4 gills on segment III, each group united basally and arranged 2 in front and 2 behind. The two outer gills of each group are smooth and tapered; the two inner ones are bipennate for more than half their length with well developed lateral pinnules. Segments III, IV and V with fine, pointed neurosetae embedded in the lateral fold. No neurosetae on segment VI. No notosetae on segment III which bears the gills. A pair of stout dorsal hooks on segment IV behind the gills. Segments V and VI with small notopodial capillaries. Segment VII and the next 12 segments bear smooth-winged notopodial capillaries and neuropodial uncini. Altogether a total of 17 thoracic setigers. Abdomen with 32 or more segments. Abdominal uncini borne on square pinnules each of which has a small superior papilla. Uncini with a single series of 5 teeth above the small rostral point and a recurved basal prow.

Augener (1914) was doubtful as to whether *I. warnebroensis* from South West Australia was identical with *I. pulchella*, but the only difference he noted was the presence of eye-spots. Specimens from Burma in the British Museum (Natural History) identified as *I. warnebroensis* are identical with *I. pulchella*. *I. sibogae* Caullery, 1944 from Indonesia is even closer for it lacks eye-spots.

I. whydaensis Augener, 1918 from tropical West Africa is a different species. A specimen in the British Museum (Reg. No. 1953 : 3 : 1 : 876) from Accra identified by Tebble 1955 has only 16 thoracic setigers of which 12 bear uncini. Moreover the branchiae are long and slender, the inner two pairs bearing numerous minute lateral pinnules which are quite different from the long paired pinnules of *I. pulchella*.

***Samythella affinis* sp. n.**

(Text-fig. 11 b-e)

RECORDS. SCD 237 (7) ; 275 (8).

DESCRIPTION. The type material (B.M.(N.H.), Reg. No. 1963.1.142-144) was obtained from station SCD 237 at 34° 51' S./23° 41' E. in 183 metres on a bottom of fine sand. Only one specimen has a complete set of gills. Complete specimens measure 10 mm. by 0.8 mm. across the anterior thorax.

The diagnostic characters may be summarised as follows : Prostomium (Text-fig. 11 e) depressed and bluntly triangular. No eyes nor glandular ridges. Buccal tentacles smooth. Buccal segment and segment II well defined. Segment III (the paleal segment) with a well developed branchial ridge bearing 3 pairs of smooth gills in a single transverse row. No median gap nor nephridial papillae on the

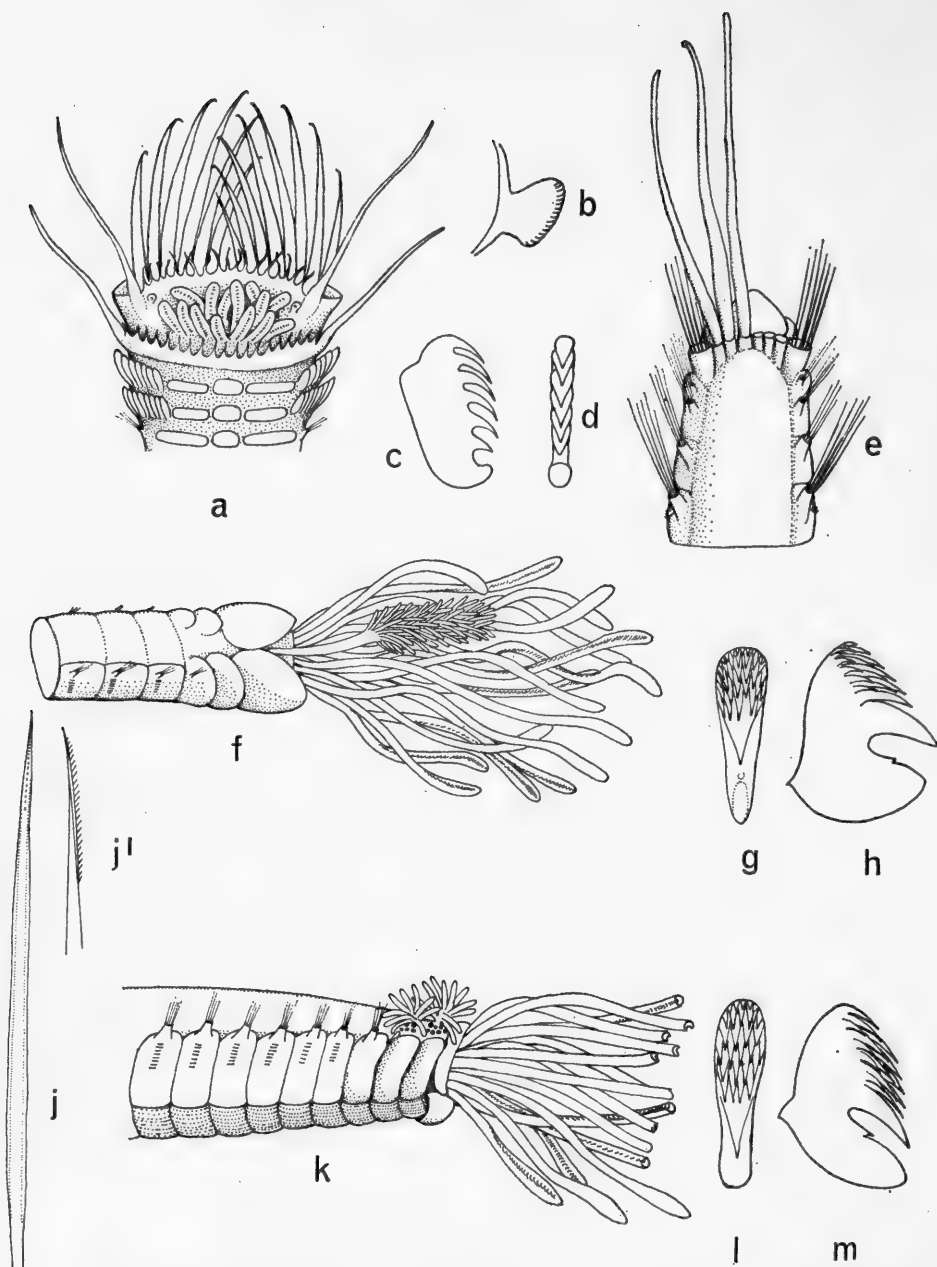


FIG. 11. *Pectinaria koreni cirrata*: (a) ventral view of head; *Samythella affinis*: (b) posterior abdominal pinnule; (c and d) lateral and face view of thoracic hook; (e) anterior end. *Pista unibranchia*: (f) dorso-lateral view of anterior end; (g and h) face-on and lateral views of hook from first row. *Amphitrite pauciseta*: (j, j') notoseta and details of tip; (k) lateral view of anterior end; (l and m) face-on and lateral views of thoracic hook.

branchial ridge. Individual gills tapered and project far in front of the prostomium. Segment III with about 10 paleae on each side of the branchial ridge. Paleae longer than normal capillaries. Segments IV and V with a small notopodia bearing a few small capillaries, segment VI with normal capillaries, segment VII and the next 11 segments with both normal capillaries and uncini. No specialised posterior notosetae. Altogether a total of 15 thoracic setigers behind the paleae. Thirteen thoracic segments with glandular ventral pads.

Eleven abdominal segments with uncini. Anterior abdominal segments with short uncigerous tori, later ones (Text-fig. 11 *b*) with uncigerous pinnules which are expanded distally. No dorsal cirri or rudimentary notopodia.

Thoracic notosetae are smooth-winged capillaries. Thoracic uncini (Text-fig. 11 *c* and *d*) with a single series of 5 teeth and a smaller attachment process above the recurved basal prow.

The generic position of this species is uncertain since there has been no uniformity in the definition of the genera. Seven genera of the subfamily Ampharetinae lack glandular ridges on the prostomium and have 3 pairs of smooth gills; they are *Amythas*, *Aryandes*, *Eusamytha*, *Glyphanostomum*, *Neosabellides*, *Samytha* and *Samythella*. Only *Aryandes* Kinberg has paleae and this is a doubtful genus of which the type species has been lost. Of the rest only *Samythella* and possibly *Eusamytha* agree in having smooth tentacles and a single row of teeth on the thoracic uncini. It is suggested that the characters of the genus *Samythella* be amended to include species with paleae. The proposed definition is as follows:

Samythella Verrill, 1873 (characters amended).

Prostomium a tongue-shaped lobe without glandular ridges. Tentacles smooth. A transverse row of 6 smooth gills on the branchial ridge formed of right and left groups of 3 each. No nephridial papilla on the branchial ridge. Segment III (the branchiferous segment) with notosetae either absent or enlarged to form paleae. Segments IV, V and VI with notopodial capillaries only. Segment VII and the next 11 segments with both notopodial capillaries and uncini. No specialised posterior notosetae. Uncini with a single row of teeth. Abdomen of 11 or more segments sometimes bearing vestigial notopodia above the uncigerous pinnules.

TYPE SPECIES. *S. elongata* Verrill, 1873.

Family TERESELLIDAE

Artacama proboscidea Malmgren, 1865

Artacama proboscidea Malmgren, 1865: 394; Hesse, 1917: 194, pl. 2, fig. 13.

RECORDS. WCD 109 (1).

NOTES. The single specimen is broken posteriorly. The main characters may be summarised as follows. Tentacular lobe horse-shoe-shaped with a dorsal notch. No eye-spots. Tentacles numerous and either broken or very short. A swollen proboscis covered with coarse papillae below the mouth opening. Segments 2 and 3 flanged but do not form lateral lobes. Three pairs of filiform gills on segments

2, 3 and 4. Each gill is a tuft of filaments arising from a basal stump. A large nephridial papilla on segment 3 and small ones on segments 6, 7, 8 and 9. Seventeen bundles of notosetae starting on segment 4. Uncini start on segment 5 and are arranged in double rows on the posterior thorax. Eleven glandular ventral pads. Abdomen incomplete but has 20 segments with large lamellar uncigerous pinnules. The base of each pinnule is constricted and the uncini are limited to part of the ventral margin. Notosetae are winged capillaries with smooth tips and the uncini are avicular with a short base, a stout main fang and a crest of about 20 denticles in 4 irregular arcs.

This is the first record of this genus from South Africa.

***Pista unibranchia* sp. n.**

(Text-fig. 11 *f-h*)

RECORDS. FAL 375 (1), 413 (12).

DIAGNOSIS. A single gill with a stalk and a terminal pom-pom of short filaments. First row of uncini without basal shafts.

DESCRIPTION. The holotype is a complete specimen measuring 10 mm. by 0.5 mm. dredged from Station FAL 413 in False Bay at 34° 12.5' S./18° 37' E. in 48 metres on sand and shell. It is colourless in alcohol and the fragile tube is encrusted with coarse sand grains.

The tentacular lobe (Text-fig. 11 *f*) is short and collarlike with numerous long grooved tentacles. Eye-spots, if present, must be few and minute. The upper lip is well developed. Glandular lateral lobes grow forward from segments 2 and 3 to form a stout sheath which supports the tentacles. The lateral lobes are unusual for they are not limited to the sides of the body but extend dorsally and ventrally practically encircling the anterior end. Small lobes also occur on segment 4. A single median gill is present on setiger 2. There is no sign of any other gills in all the thirteen specimens examined. The gill consists of a stout trunk bearing a terminal tuft of short filaments arranged in 6-7 whorls. The trunk and the tuft of filaments are about the same length.

Notosetae start on segment 4 and there are 17 bundles in all. Uncini start on segment 5 and are arranged in alternating rows on the posterior thorax. Fifteen segments with poorly defined ventral pads.

The abdomen is gently tapered and consists of about 26 long segments. The uncigerous tori are short throughout and only towards the end of the abdomen do they project as square pinnules. The pygidium is missing.

The notosetae are all broad-winged capillaries with smooth tips. The first bundle on segment 4 is rather smaller than the rest. The uncini (Text-fig. 11 *g* and *h*) are arranged in rather short rows and none of them, even those of the first row, have basal prolongations or shafts. The base is rounded, the main fang is very stout and above this is a cap of denticles arranged in 4-5 alternating close-set rows. In profile there appear to be 4-5 teeth but a face-on view shows that the dental formula is roughly MF : 4 : 5 : 7 : 10.

At first sight this species resembles a juvenile *Pista cristata* which has lost all but one of its four pom-pom shaped gills. A closer examination shows no sign of scars where the missing gills should be. The lack of shafts on the first row of uncini suggests *P. macrolobata* Hesse but this species has dichotomously branched gills. Holotype : B.M.(N.H.), Reg. No. 1963.1.153.

***Amphitrite pauciseta* sp. n.**

(Text-fig. 11 *j-m*)

RECORDS. WCD 83 (3), 85 (common).

DIAGNOSIS. This species may be recognised by the presence of pigment granules at the bases of the two pairs of gills and the possession of only 13 thoracic setigers.

DESCRIPTION. The type material consists of 9 specimens selected from station WCD 85 dredged at 33° 06' S./17° 45' E. on mud at a depth of 160 metres.

The holotype is 18 mm. long by 1.0 mm. across the thorax and is pale brown in alcohol. The tube is very fragile with adherent sand grains of various sizes. The tentacular lobe (Text-fig. 11 *k*) is collar-shaped with numerous long grooved tentacles and a few eye-spots. The lower lip is well developed. Small lateral lobes are present on segments 2, 3 and 4 but are not obvious on some of the paratypes. Two pairs of gills on segments 2 and 3. The trunk of each gill is short and the branches are digitiform so that the first impression is that each gill consists of a tuft of stout filaments. At the base of each gill there is a group of reddish subdermal spots probably associated with the vascular system. These spots were seen on every specimen examined and are very characteristic. The holotype also has a few similar spots next to the notopodium of segment 4.

Notosetae start on segment 4 and are present on 13 segments. Uncini start on segment 5 (setiger 2) and are arranged in double rows on posterior thoracic segments. A nephridial papilla is present on segment 3 just lateral to the base of the gill. Ten glandular ventral pads are present from segment 3 to segment 14.

The abdomen is tapered and consists of 42 segments. The uncigerous tori gradually lengthen to become long pinnules on the last few segments. The anus has a pleated margin.

The notosetae (Text-fig. 11 *j*) have narrow blades and end in fine, minutely serrated tips (Text-fig. 11 *j'*). The uncini (Text-fig. 11 *l* and *m*) have short bases and when seen in profile appear to have 5 indistinct teeth above the main fang ; in full face however it may be seen that there are numerous irregular arcs of denticles approximating to the formula MF : ca 5 : ca 7 : ca 9 : ca 12.

As far as I am aware this is the only species of *Amphitrite* with less than 17 thoracic setigers. Holotype : B.M.(N.H.), Reg. No. 1963.1.145.

Family **SABELLIDAE**

***Fabricia filamentosa* sp. n.**

(Text-fig. 12 *a-g*)

RECORDS. WCD 83 (2), 109 (10), 122 (2) ; SCD 223 (4).

DESCRIPTION. The holotype is a complete specimen from Station WCD 109

collected by a grab from 32° 08' S./17° 39' E. in 170 metres on a bottom of dark green mud. There are 9 paratypes.

The whole worm (Text-fig. 12 *a*) is encased in a fragile tube of flocculent debris. It is very slender measuring 4 mm. in length by 0.2 mm. broad and is colourless in alcohol. Each brancial lobe (Text-fig. 12 *b*) bears 3 radioles, each with 5 pairs of very long slender pinnules which extend like a tuft of filaments twice as far as the radiole itself. There are no palps. The whole branchial crown is about a quarter the length of the body. The collar is well developed and continuous ventrally. It is notched back dorsolaterally on each side to form a tongue-shaped median dorsal lappet but the rest of the collar is continuous and has a smooth margin. The median lappet is soldered onto a pair of dorsal lips inside the collar. A pair of conspicuous eyes is present inside the collar at the base of the branchiae. No otocysts were seen.

The slender body consists of 8 thoracic and 3 abdominal segments which differ in length. The first 3 setigers are about twice as long as broad, the 4th and 5th are longer and the 6th, 7th and 8th are about five times as long as broad. The three abdominal segments decrease in length until the third is broader than long. All abdominal segments have swollen tori while the pygidium is tapered and bears a pair of terminal eye spots.

Setiger 1 bears 4-5 narrow-bladed capillaries. The notosetae of setigers 2-8 are 4 capillaries (Text-fig. 12 *c*) with blades which are broad at the base but taper to slender tips. The neurosetae are rows of about 4 long-shafted hooks (Text-fig. 12 *d* and *e*) each with a transverse arc of about 5-7 teeth above the rostrum. In the abdomen each neuropodium bears 3 slender-bladed capillaries and the notopodium has a row of about 15 long-handled uncini (Text-figs. 12 *f* and *g*), each with 6-7 rows of teeth with 3-4 long teeth per row. Holotype: B.M. (N.H.), Reg. No. 1963.1.169.

This species is most closely related to *F. capensis* (Monro). It has a similar collar and elongated segments in the posterior thorax. The important distinctions concern the setae and the branchiae for *F. capensis* has abdominal uncini with very numerous teeth (18 rows of 8 each), thoracic uncini with 2 teeth above the rostrum and then an arc of 12-14 smaller denticles. Moreover *F. capensis* does not have such extremely elongated branchial filaments. It is a much larger worm living gregariously on the shore in sandy tubes.

Fabriciola cf. *mossambica* (Day, 1957)

Fabricia mossambica Day, 1957: 115, fig. 8 *e-o*.

RECORDS. WCD 83 (2), 108 (4); SCD 233 (4).

NOTES. These specimens are referred to the tropical East African form with hesitation, for the abdominal uncini have a greater number of teeth. They agree in the possession of filamentous palps, a triangular lobe below the mouth in place of a collar, similar thoracic setae and abdominal capillaries but the uncini have many more teeth. A juvenile had 8 rows of 4 teeth and an adult had 14 rows of 8 teeth. In *F. mossambica* there are 7 rows with 2-3 teeth per row. It is possible that this character is more variable than had been realised.

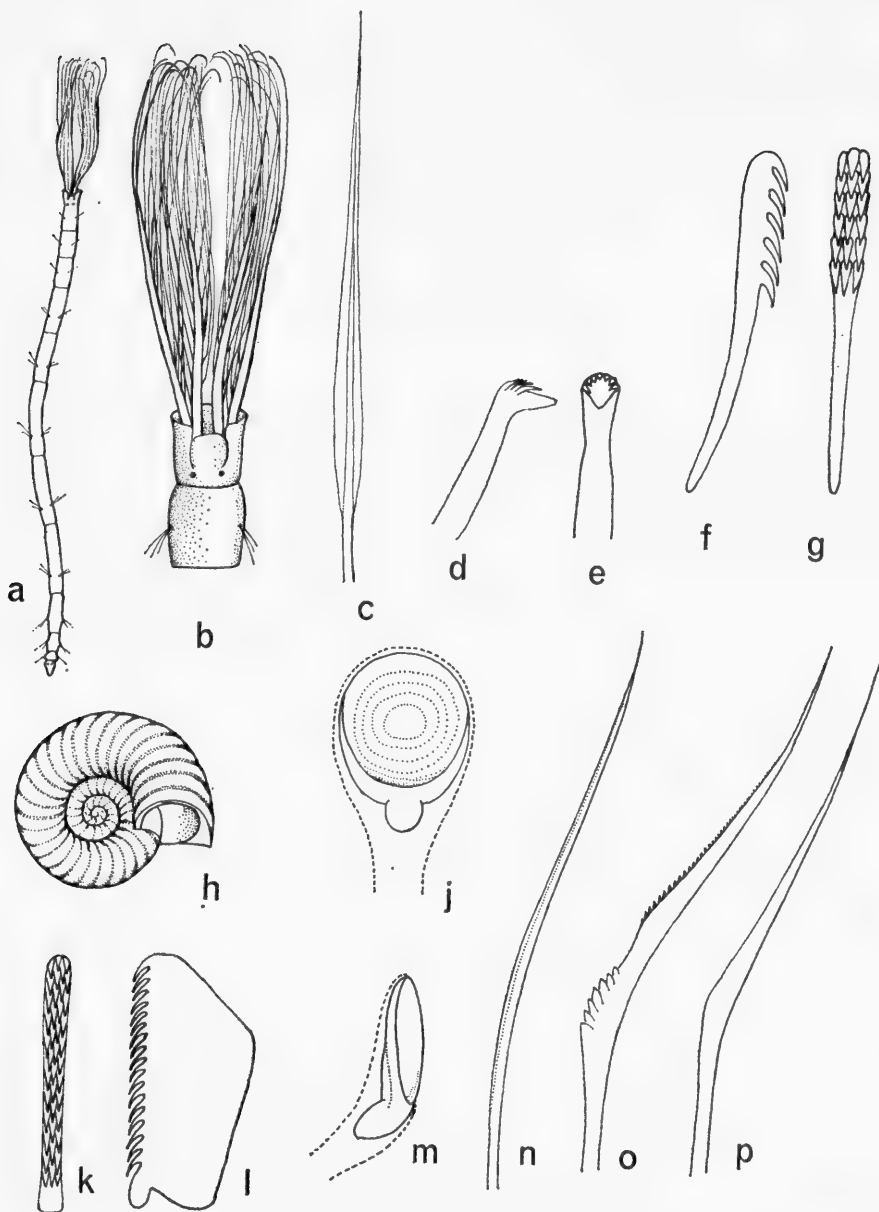


FIG. 12. *Fabricia filamentosa*: (a) entire worm; (b) head; (c) thoracic notoseta; (d and e) lateral and face-on views of thoracic hook; (f and g) lateral and face-on views of abdominal hook. *Spirorbis adeonella*: (h) tube; (j) plan view of operculum; (k and l) edge-on and lateral views of thoracic uncinus; (m) side view of operculum to show talon; (n) fine capillary from first bundle; (o) specialised collar seta; (p) smooth-winged capillary from second bundle.

According to Banse (1956) this species with its filamentous palps should be referred to the genus *Fabriciola*.

Family SERPULIDAE

Hydroides heteroceros (Grube, 1868)

Serpula (*Eupomatus*) *heteroceros* Grube, 1868 : 639.

Hydroides heteroceros : Pixell, 1913 : 75, pl. 8, fig. 2 a-c ; Fauvel, 1953 : 459, fig. 241C.

RECORDS. "William Scoresby" station WS 1022, at 25° 26' S./46° 07' E. in 58 metres on sand and shell.

NOTES. This is a new record for the area which is just south of Madagascar. *H. heteroceros* is widely distributed in the tropical Indian Ocean and the present specimens agree with Pixell's description.

Spirorbis (*Paralaeospira*) *adeonella* sp. n.

(Text-fig. 12 h-p)

Spirorbis (*Laeospira*) sp. Day, 1961 : 557.

RECORDS. SCD 154 (1) ; MB 7 (1 living).

DESCRIPTION. The additional material allows me to amplify and amend the preliminary account in 1961 of *Spirorbis* sp. The holotype was dredged in Mossel Bay growing on the calcareous Polyzoan *Adeonella* sp. at a depth of 19 metres. The shell (Text-fig. 12 h) is 1.5 mm. in diameter and is thick and vitreous with well marked annular ridges. It is coiled clockwise when viewed from above (sinistral). The operculum (Text-fig. 12 j) is oval in outline with a concave surface. The talon (Text-fig. 12 m) is a smoothly swollen knob almost at right angles to the opercular plate which is strengthened by a median ventral ridge. The branchiae consist of 7 unequal radioles with slender tips. Incubation is in the tube. The collar is well developed and the two halves overlap dorsally but are not united. There are 4 thoracic segments but the 4th is asymmetrical. Thus setiger 1 bears the collar setae, setigers 2 and 3 bear both notosetae and uncini but setiger 4 has only a short row of uncini on the concave side of the body. The abdomen is short and consists of about 13 segments.

The collar setae includes a few fine capillaries (Text-fig. 12 n) and several larger setae (Text-fig. 12 o) with very finely serrated blades and a separate dentate lobe at the base. Setigers 2 and 3 also have a few fine capillaries in addition to the numerous smooth-winged capillaries (Text-fig. 12 p). There are no "setae of *Apomatus*". The thoracic uncini (Text-fig. 12 h and l) have 2-3 rows of teeth with about 18 teeth per row. The gouge is expanded and truncate.

Two other species of the subgenus *Paralaeospira* have been recorded from South Africa, namely *S. (P.) patagonicus* and *S. (P.) capensis*. *S. (P.) adeonella* differs from both in having an annulated shell and in lacking setae of *Apomatus*. The talon is also different. Holotype : B.M.(N.H.), Reg. No. 1963.1.179.

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THIS account of the freshwater gastropod fauna of Angola is based largely on material collected by the author during the months of October and November 1957. Due to the enormous size of the territory and the short duration of the visit the collection cannot be considered to be completely representative of the Angolan snail fauna, but it includes the majority of species recorded from the area as well as several others not previously known to occur there. Wherever possible the type material of the species concerned has been examined and photographs of these specimens are included. Anatomical descriptions of the pulmonate species are given and an attempt has been made to indicate the range of morphological variation encountered in many of them, particularly those members of the Planorbidae which are known or potential intermediate hosts of the human blood-flukes. Synonymies are on a purely regional basis since it is felt that there is not yet sufficient information from the whole continent to justify more sweeping conclusions.

One of the primary objects of the expedition was to obtain topotype material of species described from Angola, but it became apparent that, due to inadequate definition of original localities, and to recent changes brought about by development of the country, this was not possible. The main effort was therefore concentrated on obtaining large samples of specimens from four regions of the country, the coastal plain in the neighbourhood of Luanda, the escarpment zone around Salazar, the northern part of the plateau around Malange and the southern area of the plateau in the Ganguelas district.

It is a great pleasure to acknowledge the assistance which I received from members of the Angolan Health Department, in particular the Director, Dr. Barrata Feio, also Dr. Pereira Nunes and all those who were so generous with their hospitality and time. Many other people, both private individuals and local administrators, contributed to the success of the field-collecting work and to all of them I am indebted as well as to Mr. D. Claugher who undertook the tedious work of making a great number of radula preparations.

The history of the malacological exploration of Angola covers just over a century. The first reports of shells of freshwater snails are those of Dunker (1845 and 1853) based on material collected by Dr. George Tams on a voyage to Lower Guinea in



the years 1841 and 1842. These collections were made only in the coastal region in the neighbourhood of Luanda and Benguela. In 1866 Morelet published a preliminary account of the molluscs collected by Dr. Friederich Welwitsch during his historic exploration of Angola between the years 1853-61 and in 1868 Morelet followed his earlier paper with a more comprehensive report of the malacological results of this expedition. Welwitsch's contribution to the exploration of Africa was quite outstanding ; a brief summary of the extent of his journeys is an essential part of this account, for it was the areas he visited that were the primary objectives of the present expedition. He arrived in Angola in 1854 and spent the first year exploring the coastal plain from Quizembo (north of Ambriz) to the mouth of the River Cuanza, a distance of about 120 miles. He then followed the course of the Rio Bengo inland for about 125 miles to Sange in the Golungo-Alto district and

spent two years based on this centre, until ill health forced him to move up to the plateau. He travelled through Ambaca to Pungo Andongo where he set up temporary headquarters and spent eight months exploring this part of the plateau region. His journeys took him to the Cuije and Lombe rivers in the east, also to the islands of Calemba in the Rio Cuanza between the cataracts of Condo and the Quissonde rapids, a distance of about 250 miles from the coast. He visited salt marshes near Quitage and the forests on the north bank of the Cuanza, then he travelled towards the Rio Luxillo to the west of Pungo Andongo before beginning his return journey to Sange. On the way back to Sange he tried to follow the Rio Lucala up into the Duque de Braganza district but his porters deserted and he was forced to abandon this part of his journey. On his return to Luanda he made a brief trip to the Libongo area near the mouth of the Rio Lifune, then, in June 1859, he travelled by sea to Benguela, stayed for a short while in the neighbourhood of the town, and went on to Mossamedes where he stayed for about two months before exploring to the south to Pinda, Cap Negro and the Bahia dos Tigres. He returned to Mossamedes and followed the Rio Mayombo inland to Bumbo and, crossing the Serra de Xella on to the plateau of Huila, he stayed for about seven months until a tribal rebellion forced him to return to the coast and thence back to Luanda and eventually to Lisbon where he arrived in January 1861.

The collection of land and freshwater molluscs which Welwitsch accumulated during the course of these journeys was the most comprehensive ever made in Angola and was one of the major contributions to African malacology in the nineteenth century.

In 1873 Sowerby described as a new species *Physa benguellensis* and gave the type locality as Benguela, Egypt. At first sight this appears to be merely another of Sowerby's regrettable lapses of geographical accuracy but the existence of a coastal village called Egito near Benguela provides a satisfactory explanation. The next contribution to the literature on the Angolan mollusc fauna was that of von Martens (1882) with descriptions of a number of terrestrial species and a new melaniid, and some years later Nobre (1905) described the collections made by Francisco Newton in 1903.

For nearly forty years nothing further was written concerning the freshwater molluscs of Angola, but in a more general work on the bulinids of Africa Bequaert and Clench (1931) included photographs of some of the paratype specimens of species described earlier by Morelet. During this period several most important works on the fauna of neighbouring territories were published and amongst these were Pilsbry and Bequaert's (1927) exhaustive monograph on the freshwater molluscs of the Belgian Congo and Connolly's (1930) paper on the non-marine Mollusca of South-west Africa. Both of these works helped to bring the existing knowledge of the Angolan fauna into perspective with that of the rest of Africa.

Interest in African freshwater snails received a considerable stimulus from Leiper's (1915) demonstration of the part played by certain members of the Planorbidae as intermediate hosts for human blood flukes of the genus *Schistosoma*, but it was not until 1942 that this influence became active in Angola with Bruno de

Mesquita's account of schistosomiasis in the territory and his publication of a list, compiled by Germain, of possible snail hosts for the parasites. Mesquita published another paper in 1953 and Sarmento wrote on a number of foci of schistosomiasis in the south in 1944, but neither of these contributed much to the knowledge of the molluscs. In 1951 the Endemic Diseases Mission started a survey of the fresh-water snails of Angola and this has resulted in several recent papers such as Azevedo and Medeiros (1956) on the anatomy of an Angolan *Biomphalaria*, Janz and Carvalho's (1956) general account of schistosomiasis in Angola with lists of mollusc species collected and, most recently, Carvalho and Janz (1960) on the Angolan species of *Bulinus*.

The province of Cabinda, although administratively a part of Angola, is separated from the rest of the territory by the Congo river and a narrow strip of the Congo Republic. It was not visited during this expedition and little is known of its mollusc fauna apart from some information in Pilsbry and Bequaert (loc. cit.) and Darteville's 1934 work on the aquatic molluscs of the principal river, the Shilloango.

Biomphalaria salinarum (Morelet)

Planorbis salinarum Morelet, 1868: p. 85, pl. 5, fig. 4.

MATERIAL. *Quissol* (2), Quastimbala stream, near Malange. 13 specimens 23rd October, 1957.

HABITAT. On aquatic vegetation in a very gently flowing part of a partially dammed stream.

SHELL (Pl. I, figs. 7, 8). All of the specimens collected were immature, the largest had about $3\frac{1}{2}$ whorls. The mean dimensions of the sample and the range (in millimetres) is maximum diameter 7.35 (3.5–9.8), umbilicus 2.35 (.88–3.32) and height 3.28 (2.45–4.37). The upper side of the whorls is slightly flattened and the lower side gently rounded without any well marked angulation. The first whorl on the upper side is deeply sunken and the umbilicus is shallow. The shells are white beneath the encrusting algae and detritus and a fine spiral microsculpture intersects the growth lines to give a granular appearance to the first $2\frac{1}{2}$ –3 whorls on the under side and, although this is present on the upper side it is not so well marked.

ANATOMY. The mantle varies in colour from creamy-white to pale grey with discrete black spots of fairly regular outline. The intermediate ridge between the kidney and rectum is well developed. The male copulatory organ is well developed in the specimens examined and the penis-sheath is approximately equal in length (occasionally a little longer) to the preputium and the penis is roughly as long as the sheath (Text-figs. 1–3). The prostatic diverticula are short and close-packed, most are divided but few have tertiary branches. The seminal vesicle consists of an upper part of complicated digitate diverticula from the hermaphrodite duct and

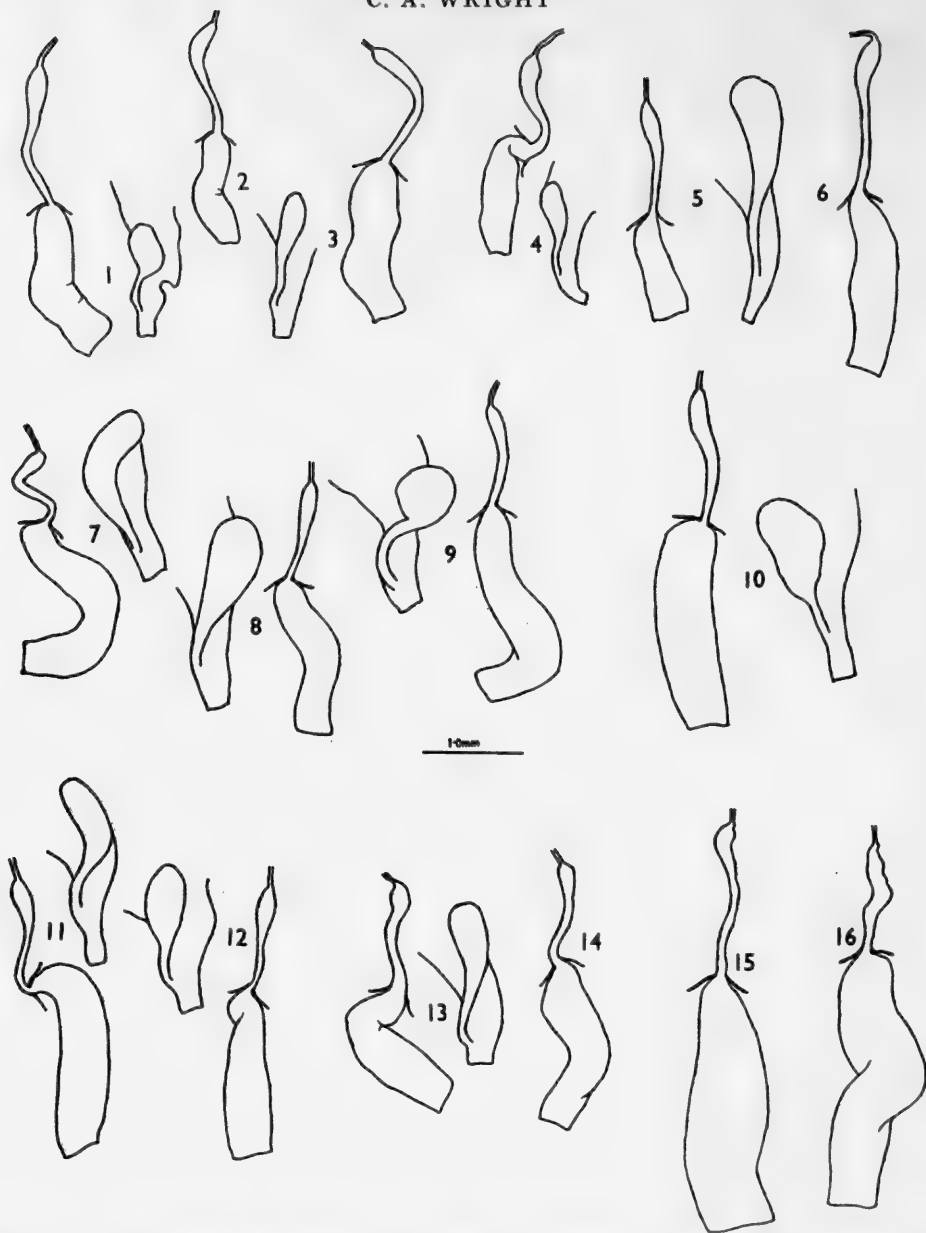
a lower portion of more regular rounded protuberances. The female reproductive system is not fully developed in this material; the receptaculum is clavate and roughly equal in length to its duct which is in turn a little longer than the vagina (Text-figs. 2, 3).

RADULA. There are about 23 teeth in each half-row of which 6–8 are tricuspid laterals. Subdivision of the endocone may occur in the fourth or fifth lateral. The endo- and mesocones of the first laterals are about equal in length, they are broad and partly fused at their bases and the tip of the mesocone is bluntly arrow-head shaped (Text-fig. 17). The ectocones of the marginals are irregularly sub-divided into several cusps of unequal size.

Biomphalaria salinarum was described by Morelet from material collected by Welwitsch from a stream near Dungo near the Rio Cuije. There is no village of this name in the area today and it was not possible to find the exact type locality but the Quastimbala stream is a tributary of the Rio Cuije and the material described here is therefore from the original district. The juvenile specimens collected do not resemble the type series (Pl. 1, figs. 1–6) closely because of the differential changes in shell form which occur with growth. However, if the ratios of shell diameter to umbilical diameter and shell diameter to height are plotted and the graphs extrapolated, the measurements for the type specimens fall close to the appropriate lines. The dimensions in millimetres of the type series are:—maximum diameter 16.3, 14.0 and 13.8; umbilicus 6.65, 5.6 and 5.4; height 4.8, 4.7 and 4.2.

The affinities of *B. salinarum* appear to be closer to the *alexandrina* species group defined by Mandahl-Barth (1957a) than to any other. The intersection of the graphs of the ratios mentioned above occurs at a shell diameter of about 13 mm. which is close to that shown by Mandahl-Barth for *B. alexandrina* and the number of whorls in the 14.0–16.3 mm. shell diameter group supports this. The broadly arrow-head shaped mesocones of the first lateral radula teeth and the subdivided ectocones of the marginals are also characteristic of the *alexandrina* group. The proportions of the male copulatory organ do not agree with those defined by Mandahl-Barth for this group in that the penis-sheath and preputium are roughly equal in length. However, Mandahl-Barth remarks that there may be differential growth of these structures and he reports immature specimens of *alexandrina* with copulatory organs resembling that of *B. rueppelli* and Abdel-Malek (1959) shows that the penis sheath in *B. boissyi* (= *alexandrina*) from Egypt is only a little longer than the preputium.

Bequaert and Clench (1933) report a series of full-grown specimens of *B. salinarum* from the Bizamba river at Boko, a tributary of the Inkisi river in the Belgian Congo and Mandahl-Barth (1957a) mentions a large, flat form of *B. pfeifferi bridouxiana* which is common in streams and rivers to the west of Katanga. Mandahl-Barth believes that this form may be *B. salinarum* but the dimensions which he quotes show that at a shell diameter of 16.5 mm. the width of the umbilicus is only a little greater than the shell height while in the type series of *salinarum* at roughly the same diameter the shell height is only about three-quarters of the umbilical width.



FIGS. 1-3. *Biomphalaria salinarum*, 1 & 3 male copulatory organs and receptacula; 2, male copulatory organ. Figs. 4-6. *Biomphalaria* sp. from Senga; 4 & 6, male copulatory organs and receptacula; 5, male copulatory organ. Figs. 7-14. *Biomphalaria pfeifferi*, 7-9, male copulatory organs and receptacula of specimens from Vila Artur de Paiva; 10, male copulatory organ and receptaculum of specimen from Cativa; 11 & 12, male copulatory organs and receptacula of specimens from the Rio Cului; 13, male copulatory organ and receptaculum of specimen from Dongo; 14, male copulatory organ of specimen from Quesso. Figs. 15 & 16. *Biomphalaria* sp. from Nova Lisboa, male copulatory organs.

Biomphalaria pfeifferi (Krauss)

Planorbis pfeifferi Krauss, 1848: p. 83, pl. 5, fig. 7.

Biomphalaria adowensis; Azevedo & Medeiros, 1956.

MATERIAL

Cangombe, Huila Province. Pools in stream bed. 10 specimens, 21st November, 1957.

Cativa, Huila Province. Washing place in Rio Cuando, 7 specimens, 23rd November, 1957.

Cului (Rio), Huila Province. Bridge on Vila Artur de Paiva-Dongo road. 4 specimens. 23rd November, 1927.

Dongo, Huila Province. Pools on margin of Rio Cubangue. 3 specimens. 23rd November, 1957.

Quesso, Huila Province. Irrigation system of Granja Administrativa. 3 specimens. 21st November, 1957.

Vila Artur de Paiva, Huila Province. 17 specimens. 21st November, 1957.

HABITAT. All of the localities from which this species was collected were either in gently flowing water or in places where the water must flow during the rainy season. The snails were always found on vegetation.

SHELL (Pl. 2, figs. 3-19). Many of the specimens collected were immature with three or less whorls, the largest were those from Cangombe. The mean dimensions in millimetres of the three larger samples are :—

	Maximum Diameter	Umbilicus	Height
Cangombe	8.95 (6.3-13.5)	3.2 (2.45-4.72)	4.3 (3.15-6.82)
Cativa	7.05 (4.2-9.8)	2.25 (1.05-3.32)	3.43 (2.97-4.2)
Vila Artur de Paiva	7.95 (3.67-10.0)	2.97 (1.22-4.02)	3.51 (2.8-3.85)

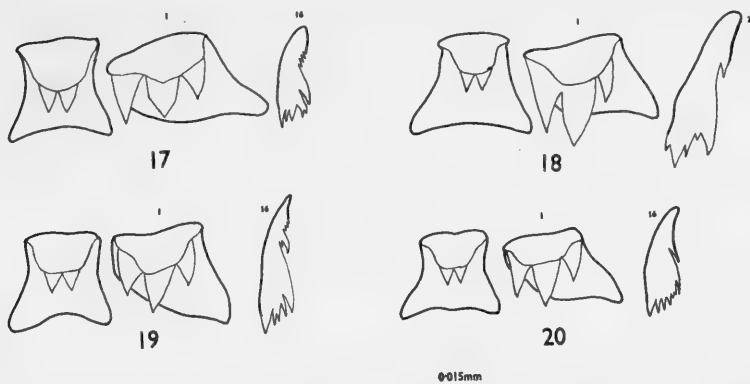
These measurements show that the shells are relatively high for their diameters (except those from Vila Artur de Paiva), and are more widely umbilicate than is usual in this species. The diameter of the whorls increases relatively rapidly and the first whorls on the upper surface are more deeply sunk than the umbilicus; they are gently rounded on the upper surface and there is a very blunt angle near the suture on the underside. The shells are pale yellowish-brown and translucent. All have a delicate spiral sculpture which intersects the growth lines to give a fine but well-marked granular appearance under high magnifications. In the specimens from Cangombe, Cativa, the Rio Cului and Vila Artur de Paiva this micro-sculpture is well developed on all whorls on both sides but in the samples from Dongo and Quesso it is better developed on the underside than on the top.

ANATOMY. The ground colour of the mantle is light grey and it is marked with spots and blotches of black of fairly regular outline. In larger individuals the right side of the mantle is more intensely pigmented than the left. The intermediate mantle ridge is well developed. The proportions of the male copulatory organ are rather variable (Text-figs. 7-14). The majority of specimens have the penis-sheath a little shorter than the preputium but in some of the smaller specimens the sheath is only about two-thirds or half the length of the preputium. The penis is roughly

equal in length to the sheath but in a few individuals it is slightly longer and extends into the preputium. The seminal vesicle in most individuals has a complicated system of digitate diverticula similar to the upper part of the vesicle in *B. salinarum*. The receptaculum seminis is so variable in shape according to the maturity of the individual specimens that it can have little taxonomic significance (Text-figs. 7-13). In general it is pyriform and the dilated part is about half as long again as the duct.

RADULA. The number of teeth in each half-row varies between 19 and 25, and there are 6-8 tricuspid laterals on each side of the central. These figures do not appear to vary much with the size of the individual. There are some differences in the characters of the cusps of the laterals, in the majority of specimens the mesocone of the first laterals is triangular (Text-fig. 19) but in some it is slightly arrow-head shaped. Most of the individuals have the endo- and mesocone of the first laterals roughly equal in length but two specimens (one from Cangombe and one from Quesso) have the mesocone distinctly longer while in two others (Dongo and Quesso) the endocone is the larger cusp. One of the specimens from the Rio Cului had the cusps of the first laterals distinctly broader and shorter than in any of the other specimens. The ectocone of the marginals is sometimes single and sometimes subdivided, but this is a character which varies considerably in the same radula and the undivided condition seems to be the commonest.

Biomphalaria pfeifferi is a widespread and variable species which has so far not been recorded with certainty in Angola. Azevedo and Medeiros (1956) described the anatomy of a species which they called *B. adowensis* from Bailundo near Nova Lisboa in Huambo Province and considered that this form was different from *B. pfeifferi* from Mocambique. However, Schutte and van Eeden (1959) suggest that *B. adowensis* cannot be regarded as distinct from *B. pfeifferi* and Mandahl-Barth (1957a) considers that it is doubtful if *B. adowensis* and *B. pfeifferi rueppelli* (Dunker), are different. In the same paper Mandahl-Barth mentions the occurrence of a small species of *Biomphalaria* from the Chibia district (Huila Province) of Angola in which the shell resembles that of typical *pfeifferi* but in which the anatomical characters are closer to those of *B. p. rueppelli*. More recently Mandahl-Barth (1960) has suggested that all of the forms which he had earlier regarded as subspecies of *B. pfeifferi* (with the exception of *B. rhodesiensis*) should no longer be considered distinct but should be regarded as variants of a single species. The description given by Azevedo and Medeiros (1956) might well apply to some of the specimens examined in this work and there is no doubt that the proportions of the male copulatory organ described here are closer to those of *rueppelli* from Ethiopia (Wright and Brown, 1962) than they are to those of *pfeifferi* from South Africa (Schutte and van Eeden, 1960). Similarly, the shape of the lateral radula teeth is more like that of *rueppelli* than that of *pfeifferi* but the subdivision of the ectocone of the marginals is extremely irregular and in this respect agrees both with Schutte and van Eeden's (1959) observations in *pfeifferi* and Wright and Brown's (1962) finding in *rueppelli*. Until a much more extensive study of the African members of *Biomphalaria* has been carried out it is not possible to be certain of the affinities of any particular group of populations.



FIGS. 17-20. Radula teeth of *Biomphalaria*. Fig. 17. *Biomphalaria salinarum*. Fig. 18. *Biomphalaria* sp. from Nova Lisboa. Fig. 19. *Biomphalaria pfeifferi*. Fig. 20. *Biomphalaria* sp. from Senga.

Biomphalaria sp. (1)

MATERIAL. *Senga, Huila Province*, stream near village, 5 specimens, 22nd November, 1957.

HABITAT. The snails were found on aquatic vegetation in gently flowing water.

SHELL (Pl. 1, figs. 9, 10). The shells are more depressed and more broadly umbilicate than those of *B. pfeifferi* and the whorls do not increase in size so rapidly, they are almost flattened on top and slightly carinate beneath on at least the first three whorls. There is a well-marked spiral micro-sculpture on the underside extending well on to the third whorl. The three largest specimens (all just under four whorls) are about 8 mm. diameter, 2.8 mm. high and have an umbilical diameter of about 2.8 mm. The colour is light reddish-brown and the growth lines are irregular giving a rather rugose appearance.

ANATOMY. Three of the five specimens were dissected. The characters of the mantle are in no way remarkable. The male copulatory organ is a little longer and more slender than in *B. pfeifferi* and the sheath is either longer than or at least equal to the preputium in length (Text-figs. 4-6). The prostate is longer and the diverticula are less closely packed than in *B. pfeifferi*. The vesicula seminalis has only smoothly ovoid protuberances and is thus similar to the lower part of the vesicle in *B. salinarum*. The receptaculum seminis is clavate and the dilated part is about equal in length to the duct (Text-figs. 4, 6).

RADULA. There are 18-24 teeth in each half-row of which 7 or 8 are tricuspid laterals. The mesocones of the laterals are triangular and the endocones of at least the first laterals are as long or longer than the mesocones and they are sharply pointed. The majority of the marginal ectocones are undivided (Text-fig. 20).

No attempt has been made to allocate this material to any known species because there are not enough specimens for a sufficiently detailed description to be made. Apart from their small size the shells show a similarity to those of the *alexandrina* group in their general form. The proportions of the male copulatory organ are more similar to those of the *sudanica* group and the characters of the radula would certainly not preclude the inclusion of these specimens in that group. It is possible that this sample represents a slightly aberrant form of *B. rhodesiensis* but speculation on its affinities is not likely to be constructive. The point of interest is that the sample comes from an area in which *B. pfeifferi* is generally distributed and there is no doubt that this form differs from that which is locally dominant.

Biomphalaria sp. (2)

MATERIAL. *Nova Lisboa, Huambo Province.* Sample provided by Dr. Morais de Carvalho, no further details available. 23 specimens.

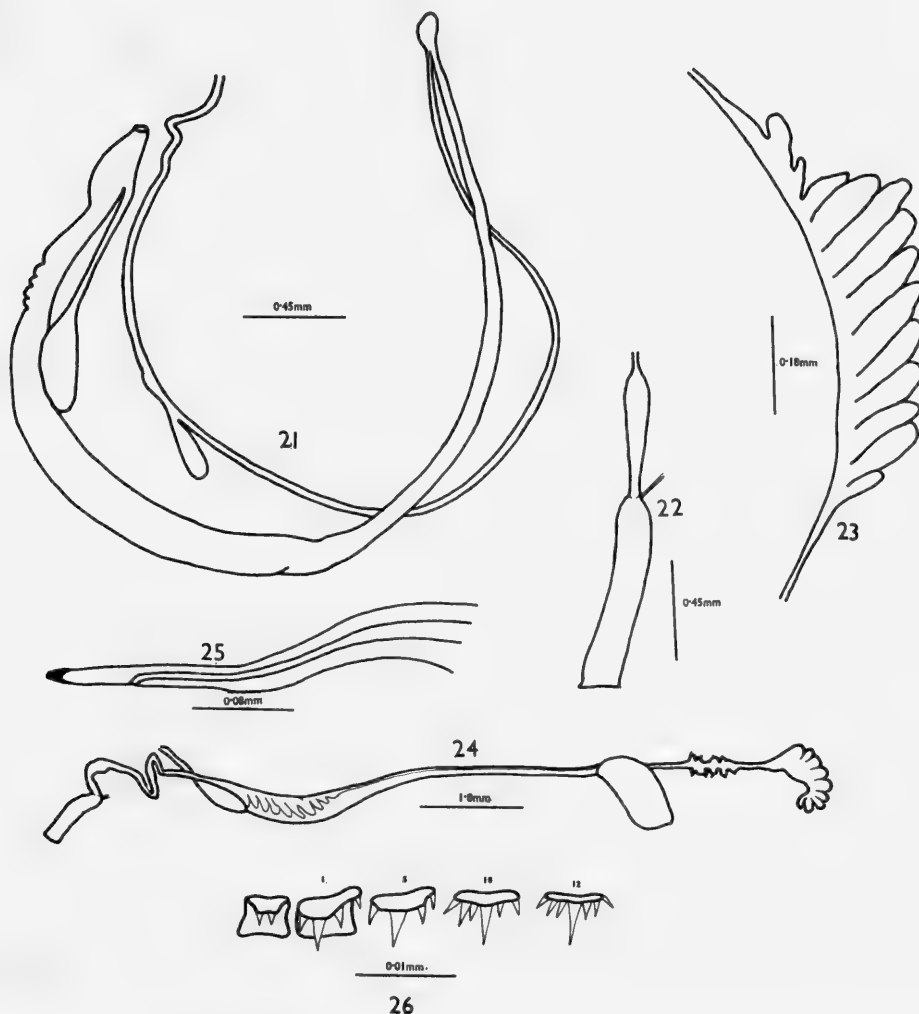
SHELL (Pl. 2, figs. 1, 2). The sample is fairly uniform in size, the mean dimensions and range in millimetres being, diameter 13.7 (12.7–14.9), height 5.1 (4.55–6.1) and umbilical diameter 4.9 (4.7–5.25). The shells are higher than those of *B. salinarum* and the whorls are more rounded, showing no carination. The fine spiral micro-sculpture extends well on to the third whorl on the underside but is more restricted on the upper surface. The colour of the shells is light brown.

ANATOMY. Unfortunately none of the specimens was sufficiently well preserved to allow a full study of the anatomy. The male copulatory organ is large and the penis-sheath is about half as long as the preputium (Text-figs. 15, 16). The penis extends just into the preputium and its tip is often bent but this may be a fixation artefact.

RADULA. The radula differs from those of all of the other *Biomphalaria* examined in this work by the long dagger-like mesocones of the lateral teeth being united at the base with the sharply pointed endocones of nearly equal length and by the ectocones being much shorter. There are 25–28 teeth in each half-row, of which 13–15 are tricuspid laterals. The ectocones of the marginals are undivided, almost without exception (Text-fig. 18).

The affinities of this form are not readily determined. If the ratios of umbilical diameter to shell diameter and height to shell diameter are plotted a random distribution of the points is obtained around the mean shell diameter of 13–14 mm., suggesting an intersection of the lines for these two ratios at about this size. This character suggests a relationship to the *alexandrina* group, but the proportions of the male organ (which may be unreliable due to poor fixation) are more like those for the *pfeifferi* group. The form of the radula is unlike that of any of the others examined in this study but it has possible affinities with the *alexandrina* group. More material

from the central plateau region must be studied in great detail before conclusions about the relationships of this form can be made, but it is possible that it may have affinities with the large, flat form of *B. pfeifferi bridouxiana* described by Mandahl-Barth (1957a) from rivers in the Congo and mentioned in the discussion of *B. salinarum*.



FIGS. 21-26. *Anisus misellus*. Fig. 21. Part of genital system showing uterine glands, receptaculum and aberrant prostate consisting of a single diverticulum. Fig. 22. Male copulatory organ. Fig. 23. Normal prostate. Fig. 24. Whole genital system. Fig. 25. Tip of penis showing cap-like cuticular stylet and sub-terminal opening of vas deferens. Fig. 26. Radula teeth.

Anisus misellus (Morelet)

Planorbis misellus Morelet, 1868: p. 85, pl. 5, fig. 5.

MATERIAL

Panguila (Lagoa), lake near mouth of the Rio Bengo. 36 specimens. 8th November, 1957.

Quifangondo, marsh on the bank of the Rio Bengo. 12 specimens. 16th November, 1957.

Lalama (Lagoa), lake near junction of Rio Calucala and Rio Bengo. 11 specimens. 14th November, 1957.

Bom Jesus, small lake on bank of Rio Cuanza. 4 specimens. 13th November, 1957.

Dondo, Rio Mucoso (included in sample of *B. forskali* received from Dr. Morais de Carvalho). 3 specimens. 3rd July, 1957.

Quionqua (2), small pool beside road. 9 specimens. 24th October, 1957.

HABITAT. This species was found in habitats ranging from a small stagnant pool to pools in a floating marsh and on aquatic plants in large lakes but not (with the possible exception of the material from Dondo whose habitat is not known) in flowing water.

SHELL (Pl. 3, figs. 25, 26). Small, flattened, largest specimens with 4-4½ whorls which increase slowly in size and scarcely overlap one another. The shells are almost completely flattened beneath and slightly concave above but in some individuals this may be reversed. The lower edge of the periphery is bluntly angulate, the aperture is sometimes slightly raised and the sutures are shallow. The colour varies from reddish- to pale yellowish-brown and the sculpture consists of fine growth lines and an irregular punctation with fine spiral lines which are particularly well marked on the underside. The largest specimens seen are about 5 mm. diameter and 1.2 mm. high.

ANATOMY. The mantle is very light grey, almost white, with sparse grey markings and a grey-blue border. The pseudobranch consists of two relatively large flaps attached to the anal lobe. The male copulatory organ is slender, the penis sheath is narrow, slightly dilated proximally and about half the length of the preputium which is roughly twice as wide as the sheath (Text-fig. 22). The penis is a little longer than the sheath and is tipped with a very small, cap-like cuticular stylet (Text-fig. 25), the opening of the vas deferens is subterminal. The vas deferens is not exceptionally long and the prostate, consisting of about a dozen simple diverticula, is closely applied to the uterus (Text-fig. 23). Several of the specimens which were examined had only a single large prostatic diverticulum (Text-fig. 21). The sperm duct is long and straight and the convolutions of the seminal vesicle on the hermaphrodite duct have numbers of small protuberances. The vagina is short and dilated into an ovoid vaginal bulb into which opens the long duct of the receptaculum seminis (Text-fig. 21). The receptaculum is ovoid and about half the length of its duct. The uterus is long and narrow and has a series of corrugations near to its junction with the vagina but it is otherwise straight and grades almost

imperceptibly into the straight oviduct. The albumen gland is relatively small (Text-fig. 24).

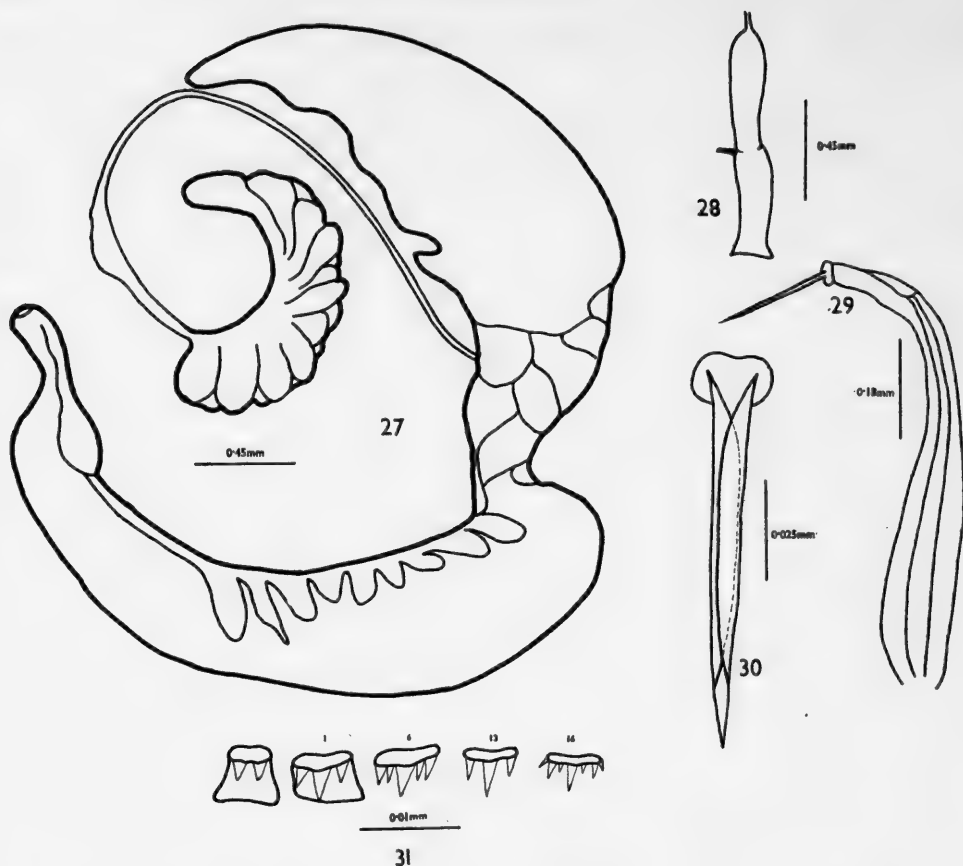
RADULA. The radula teeth are small, the centrals are bicuspid and the first five laterals are basically tricuspid but usually with a very small fourth cusp high up outside the ectocone. There are about eight marginal teeth in each half row and these are six- or seven-cusped, with a large narrowly pointed mesocone and smaller lanceolate cusps on either side of it (Text-fig. 26).

The type locality for *A. misellus* is the Lagoa Quilunda from which no specimens were obtained during this investigation. However, Lagoa Lalama is a short distance up-stream on the Rio Bengo from Quilunda and Lagoa Panguila and the marsh at Quifangondo are a few miles down-stream on the same river so that some of the material described here is from very close to the type locality. The present specimens compare well with those in the type series although the punctate pattern is not easy to make out on the original material (Pl. 3., figs. 19-24).

This species has been generally regarded as synonymous with *A. natalensis* (Krauss) but the anatomy of *natalensis* has recently been described (Wright and Brown, 1962) and the structure of the male copulatory organ in the two species is quite different, also the punctate shell sculpture on *misellus* does not appear to have been reported on *natalensis*. In *natalensis* the terminal part of the penis is sclerotised progressively towards the tip and the vas deferens opens almost terminally with a group of backwardly directed spines surrounding its aperture, while in *misellus* the penis-tip bears a minute but distinct cap-like stylet and the vas deferens opens well back from the end.

Binder (1958) has described the anatomy of *Gyraulus gibbonsi* from the Ivory Coast and the structure of the penis in this species and *misellus* is very similar. The stylet in *gibbonsi* appears to be more sharply pointed and the opening of the vas deferens is closer to the penis tip, also the penis is longer, extending about half way into the preputium. According to Binder, the prostate in *gibbonsi* is a long tubular structure without diverticula, a most unusual feature in the Planorbidae, but this is possibly an extreme development of the single prostatic diverticulum found in some specimens of *misellus*. The length of the receptaculum seminis duct appears to be relatively shorter in *gibbonsi* than in *misellus* and Binder shows the vesicula seminalis to be smooth and without tubercles. The cusps of the radula teeth in *gibbonsi* are broader and less lanceolate than those in *misellus* and the mesocones of the marginals are less prominent. These differences seem to justify the retention of these two forms as separate species for the time being but Hubendick (1957) has shown that individual variation in this type of penis structure in *Anisus crista* can be considerable. One fact, however, is certain, and that is that both the Ivory Coast form and the species from Angola are distinct from *A. natalensis*.

The generic and sub-generic nomenclature in this group of small planorbids is at present very confused and must await the study of more material before it can be clarified. If the characters of the penial stylet are to be used as a basis for grouping the species then *misellus* and *gibbonsi* belong in the *crista* group (placed by Hubendick in the sub-genus *Armiger*) while *natalensis* must stand on its own.



FIGS. 27-31. *Gyraulus costulatus*. Fig. 27. Whole genital system without male copulatory organ. Fig. 28. Male copulatory organ. Fig. 29. Penis showing stylet and sub-terminal opening of vas deferens. Fig. 30. Penial stylet. Fig. 31. Radula teeth.

Gyraulus costulatus (Krauss)

Planorbis costulatus Krauss, 1848: p. 83, pl. 5, fig. 8.

MATERIAL

Dongo, Rio Cubangue, Huila Province. 10 specimens. 23rd November, 1957.

Cangombe, stream, Huila Province. 6 specimens. 21st November, 1957.

Cului (Rio), at bridge on road from Dongo to Vila Artur de Paiva, Huila Province. 2 specimens. 23rd November, 1957.

Cativa, Rio Cuango, Huila Province. 5 specimens. 23rd November, 1957.

Gunda-Vunjanga, Huila Province. 1 specimen. 22nd November, 1957.

Moembege (Rio), Agricultural Research Station, Salazar. 3 specimens. 29th October, 1957.

Quissol (2), Quastimbala stream (near Malange). 2 specimens. 23rd October, 1957.

HABITAT. The only consistent feature about the six localities in which this species was found is that in all of them the water was either flowing or was a more or less static pool in a stream bed which would contain flowing water during the wet season. None of the samples was found in truly stagnant or heavily polluted water and most of the habitats had almost complete sun exposure.

SHELL (Pl. 3, figs. 27-30). 3-3½ whorls rapidly increasing in size, upper side convex, lower concave, a variable basal angle at the periphery of the outer whorl. Many of the shells are heavily coated with algae and deposits, the colour of the shell itself is whitish, it is strongly and slightly irregularly ribbed and the degree of ribbing varies somewhat between populations. No other sculpture was observed.

ANATOMY. Mantle light grey to almost white, a moderately well-developed simple pseudobranch lobe is present. The male copulatory organ is short, the proportions of the penis sheath and preputium vary slightly but they are usually about equal in length and roughly equal in width, the preputium being a little wider than the main part of the sheath (Text-fig. 28). The penis varies in length, it may extend well into the preputium or only just reach the junction between the preputium and sheath. The tip of the penis is equipped with a well-developed dagger-like stylet the base of which is discoidal and the edges of the blade are rolled over to form a channel which opens near to the tip of the stylet (Text-fig. 30). The vas deferens opens a short distance from the end of the soft part of the penis and a groove from the opening leads down to the channel in the stylet (Text-fig. 29). The vas deferens runs back to the prostate which has about nine short and rather irregular wide diverticula and is closely applied to the proximal end of the glandular uterus. The sperm duct is short and the vesicula seminalis is a simple asymmetrical swelling near to the proximal end of the hermaphrodite duct. The vagina is short and slightly dilated to form a vaginal bulb, the receptaculum seminis duct opens into the bulb, the receptaculum is club-shaped and about equal in length to its duct. The oöthecal and muciparous glands surrounding the uterus are massive and the oviduct is strongly convoluted. The albumen gland is very large (Text-fig. 27).

RADULA. The radula teeth are small, the centrals are bicuspid, the first five laterals are tricuspid and the remaining twelve to fourteen teeth in each half-row show a gradual increase in the number of cusps until the extreme marginals have about seven (Text-fig. 31). The cusps are broader and less needle-like than those of *Anisus misellus* but otherwise the teeth are very similar in the two species.

G. costulatus was originally described from Natal but there are records of its occurrence in many areas in Africa and it is in no way surprising that it should also be found in Angola. The anatomy of this species has been described by Ranson (1955) and Azevedo et al. (1957), in both cases the descriptions are based on material

from the Sul do Save province of Mozambique and they compare well with the present material. The close similarity in the illustrations of the two published descriptions does not give an indication of individual variation within the species.

The structure of the stylet in this species is similar to that described by Baker (1945) for several species of *Anisus* (including the genotype, *A. spirorbis*) and *Gyraululus* and it agrees in general structure but not in detail with that described by Hubendick (1958) for *Gyraululus trapezoides*.

Lentorbis benguelensis (Dunker)

Planorbis benguelensis Dunker, 1845: p. 8, pl. 2, figs. 1-4.

MATERIAL

Lalama (Lagoa), lake near junction of Rio Calucala and Rio Bengo. 6 specimens. 14th November, 1957.

Panguila (Lagoa), north-west corner of lake near the mouth of the Rio Bengo. 2 specimens. 9th November, 1957.

Quifangondo, marsh on banks of Rio Bengo. 3 specimens. 16th November, 1957.

HABITAT. The specimens from Lalama were collected together with *Segmentorbis kanisaensis* and *Anisus misellus* in the reed bed fringing the lake, those from Panguila were found with *A. misellus* and *B. forskali* on lily leaves and *Ceratophyllum* and the material from Quifangondo was taken together with *A. misellus* in small pools in a floating marsh.

SHELL (Pl. 3, figs. 15, 16). Lenticular, upper side convex, more or less flat beneath, lower angle gently curved, whorls overlapping one another, umbilicus narrow, colour pale yellowish-brown, very fine growth lines and fine spiral sculpture, most marked on the underside. Five of the Lalama specimens and two of those from Quifangondo had small internal septa, either one or two sets in the last whorl. The basal lamella in each set is relatively short, extending about half to two-thirds of the width of the whorl, the inner one curves over the inner wall and projects well into the lumen of the whorl. The outer lamella is short and more or less straight on the steepest part of the outer wall while the dorsal is a simple circular protuberance and is not always present (Text-figs. 34, 35). The dimensions of the largest specimen (from Lalama) were :—diameter, 4.9 mm., umbilicus 1.3 mm. and height 1.82 mm.

ANATOMY. All of the specimens except the two smallest from Lalama were dissected, six were aphyallid and of the three with copulatory organs two were grossly infested with sporocysts of an unidentified furcocercous cercaria and the third contained many metacercarial cysts. As a result no complete genital system was obtained intact and this description is based on a composite picture derived from several individuals.

The mantle is greyish-white with darker markings along the edges of the kidney which is narrow proximally and widens toward the anterior end. No ridges were

observed on the underside of the mantle. The male copulatory organ is large, the sheath is a little longer and only slightly narrower than the preputium, the maximum diameter of the proximal dilatation of the sheath is about equal to the diameter of the preputium (Text-fig. 38). The penis is long, about equal in length to the combined lengths of the sheath and preputium and it lies coiled within the sheath. The upper part of the preputium contains a large, glandular lobe in addition to the usual two muscular pillars. The vas deferens is long and convoluted, in aphyallid specimens where no prostate is developed it is often present but it is narrow and straight. The prostate consists of about twelve irregularly shaped diverticula and it lies well back, closely applied to the proximal glandular part of the uterus (Text-fig. 39). The vagina is short and leads into the long uterus, the distal part of which is slightly convoluted and surrounded by a yellowish-orange oöthecal gland while the proximal part is straight and surrounded by a translucent white muciparous gland. The receptaculum seminis is small and club-shaped, the duct is about equal in length to the sac (Text-fig. 40). The vesicula seminalis is little more than a dilatation of the hermaphrodite duct and does not appear to have marked protuberances.

RADULA. The teeth are extremely small and it is difficult to make out their structure with accuracy. The centrals are bicuspid and the first seven teeth in each half row appear to be only tricuspid but there is a possibility of very fine interstitial cusps on either side of the mesocone. The remaining eleven teeth in the half row are at least five-cusped, the mesocone dominating (Text-fig. 42).

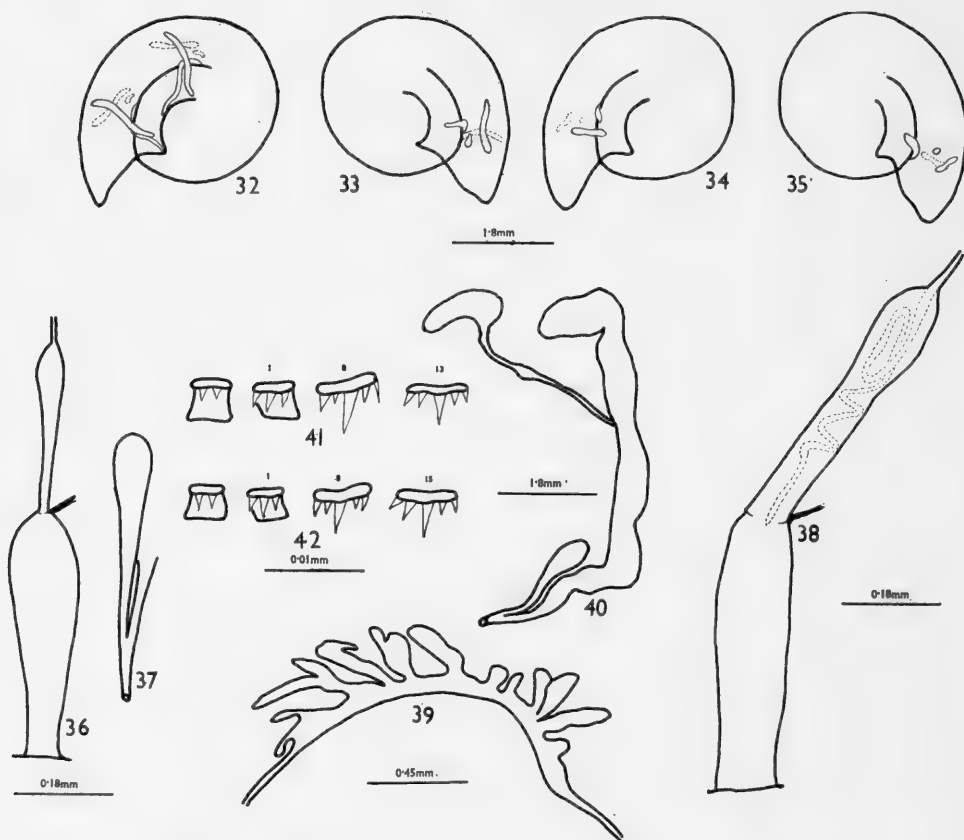
Planorbis benguelensis was described by Dunker from shells collected in the region of Benguela. Two of his original specimens from the Berlin Museum have been examined (Pl. 3, figs. 5–10) and the present material agrees well with them except that the original specimens are larger (6.9 and 6.0 mm. diameter) and have no trace of internal lamellae.

P. benguelensis was referred to *Hippeutis* by Pilsbry and Bequaert (1927) but in 1954 Mandahl-Barth showed that the other African species placed in *Hippeutis*, *H. junodi* Connolly, 1922, was anatomically distinct from the Palaearctic members of the genus and he created the genus *Lentorbis* for the two African species with *benguelensis* as type species.

The large proportion of specimens with internal lamellae in the present material appears to be unusual. Mozeley (1939) reported finding a species of *Hippeutis* in Tanganyika which resembled *junodi* but for the presence of a small tooth in the final whorl of some specimens, a character not mentioned by Connolly in his original description of the species or illustrated by him in the figure published later (Connolly, 1925). However, examination of the type series (Pl. 3, figs. 1–4) of *junodi* shows that four out of the seven specimens have at least one basal lamella in the body whorl.

The anatomy of *L. junodi* has been described briefly by Mandahl-Barth (1954) and more fully by Azevedo, Medeiros and Costa Faro (1957). There are several fairly clear anatomical differences between *benguelensis* and *junodi*. The male copulatory organ of *junodi* is illustrated by Azevedo et al. as having the sheath at

least twice as long as and, apart from the proximal dilation, as being very much narrower than the preputium. In *benguelensis* the sheath and preputium are more nearly equal in length and diameter. The receptaculum seminis in *junodi* is very large and sac-like, extending right back to the level of the albumen gland while that in *benguelensis* is much smaller, ovoid and extends posteriorly only about half way up the length of the oöthecal gland. There are some differences also in the form of the radula teeth illustrated by Azevedo et al. and those seen in specimens of *benguelensis* but because of the minute size of the teeth and the possibility of misinterpreting their detailed structure it is perhaps best not to emphasize these differences.



FIGS. 32 & 33. Shell of *Segmentorbis kanisaensis* showing internal lamellae. Fig. 32. Ventral view. Fig. 33. Dorsal view.

FIGS. 34 & 35. Shell of *Lentorbis benguelensis* showing internal lamellae. Fig. 34. Ventral view. Fig. 35. Dorsal view. Fig. 36. *S. kanisaensis*, male copulatory organ. Fig. 37. *S. kanisaensis*, receptaculum. Fig. 38. *L. benguelensis*, male copulatory organ. Fig. 39. *L. benguelensis*, prostate. Fig. 40. *L. benguelensis*, whole genital system of aphyllid specimen. Fig. 41. *S. kanisaensis*, radula teeth. Fig. 42. *L. benguelensis*, radula teeth.

Segmentorbis kanisaensis (Preston)

Segmentina kanisaensis Preston, 1914: p. 265, pl. 18, figs. 17-19.

MATERIAL

Lalama (Lagoa), lake near junction of Rio Calucala and Rio Bengo. 7 specimens. 14th November, 1957.

Quequesse (Lagoa), lake on Cuanza flood plain. 1 specimen. 13th November, 1957.

HABITAT. In the reed-bed fringing the lake, collected together with *Anisus misellus* and *Lentorbis benguelensis*.

SHELL (Pl. 3, figs. 17, 18). Flattened, lenticular, upper side convex, lower side almost flat, basal angle sharp forming a slight carination, whorls overlapping one another and umbilicus narrow. The shells are light yellowish or almost colourless and the sculpture consists of fine growth lines and very fine spiral lines on the under side and an extremely fine pitting on the upper surface. The aperture is slightly deflected downward. All of the shells are internally septate with two or three sets of lamellae except the smallest which has only one set. The basal lamella extends almost the whole width of the body whorl and is slightly S-shaped, the inner lamella curves downward anteriorly over the inner wall of the whorl and runs forward along the inner angle of the suture for a short distance. The outer lamella curves over the upper outer angle of the whorl and the dorsal consists of a simple comma- or lozenge-shaped protuberance (Text-figs. 32, 33). The largest specimen in the sample had a diameter of 4.2 mm., umbilicus 1.27 mm. and height 1.27 mm.

ANATOMY. Three specimens were dissected of which two proved to be aphyllid. The mantle is fairly uniformly spotted with dark grey except over the kidney where the colour is lighter. The male copulatory organ is relatively large, the penis sheath is slender with a slight proximal dilatation and it is about equal in length to the preputium which is much wider (Text-fig. 36). The vas deferens is long, thin and sinuous and the prostate resembles that in *Lentorbis benguelensis*. There are no nodules on the seminal vesicle which is a simple dilatation of the hermaphrodite duct about half way along its length. The female genital system resembles that of *L. benguelensis* except for the receptaculum which is slightly club-shaped and merges gradually with its duct (Text-fig. 37).

RADULA. As in *L. benguelensis* the teeth are extremely small and no significant differences have been observed between the two species except that there are fewer in each half row in *kanisaensis* (1+5+8) than in *benguelensis* (1+7+11) (Text-fig. 41).

Mandahl-Barth (1954) separated the African species placed in *Segmentina* from the Palaearctic members of the genus and created for them the genus *Segmentorbis* with *S. angusta* Jickeli as type species. The basic anatomical difference between *Segmentina* and *Segmentorbis* is that there are two flagellae on the penis of *Segmentina* and only one in the African genus. For *S. kanisaensis* which lacks a flagellum

altogether Mandahl-Barth created the sub-genus *Carinorbis* but this name was pre-occupied and in 1956 he proposed the new sub-generic name *Acutorbis*.

Originally described from the southern Sudan, *S. kanisaensis* (Pl. 3, figs. 11-14) has been reported from Uganda and Tanganyika by Mandahl-Barth (1954), from South Africa by Connolly (1939), from the Gambia by Smithers (1956) and from the Ivory Coast by Binder (1957) and thus seems to have an extremely wide distribution which is further extended by this record from Angola.

With the small amount of material which has been available for this study it is not possible to draw major conclusions as to the status of the genera *Lentorbis* and *Segmentorbis* but further work may show that the two are not clearly distinct.

***Bulinus globosus* (Morelet)**

Physa globosa Morelet, 1866: p. 162.

Physopsis globosa Morelet, 1868: p. 93, pl. 9, fig. 4.

MATERIAL

- Fazenda Tentativa*, sugar plantation near the mouth of the Rio Dande. Two localities: (1) stream carrying effluent from sugar refinery, 22 specimens; (2) irrigation ditches on the plantation, 41 specimens. 8th November, 1957.
- Matoz (Lagoa)*, drainage ditch beside small lake on the edge of Fazenda Tentativa. 37 specimens. 8th November, 1957.
- Libongo (Fazenda)*, irrigation ditches on oil palm plantation near mouth of Rio Lifune. 12 specimens. 9th November, 1957.
- Quilunda (Lagoa)*, large lake on the banks of the Rio Bengo. 35 specimens. 14th November, 1957.
- Lalama (Lagoa)*, lake near junction of Rio Calucala and Rio Bengo. 7 specimens. 14th November, 1957.
- Lumango (Lagoa)*, lake near Rio Bengo. 2 specimens. 14th November, 1957.
- Panguila (Lagoa)*, large lake near mouth of Rio Bengo. 4 specimens. 8th and 9th November, 1957.
- Bom Jesus*, small lake on the banks of the Rio Cuanza. 10 specimens. 13th November, 1957.
- Cabungabunga (Lagoa)*, large lake on the flood plain of the Rio Cuanza. 8 specimens. 13th November, 1957.
- Dalagosa (Lagoa)*, lake on flood plain of Rio Cuanza. 189 specimens. 13th November, 1957.
- Guimbe (Lagoa)*, large lake near Rio Cuanza. 4 specimens. 13th November, 1957.
- Quequesse (Lagoa)*, grass-choked swamp on flood plain of Rio Cuanza. 5 specimens. 13th November, 1957.
- Moembege (2) (Rio)*, two localities: (1) backwater about one kilometre upstream from Salazar, 4 specimens; (2) Washing point in river in Salazar, 5 specimens. 30th November, 1957.

Quionqua (1), marshy roadside pool about two kilometres north of village on road to Duque de Braganza falls. 31 specimens. 25th October, 1957.

Quissol (2) (*Fazenda*), dammed pool in Quastimbala stream. 8 specimens. 24th October, 1957.

HABITAT. This species is extremely common throughout the coastal plain and was also found in the escarpment region at Salazar and on the plateau in the Malange district. In these areas *B. globosus* was found in a wide variety of habitats, large lakes, small pools (some possibly temporary) and in gently moving water in irrigation ditches and small rivers. The species is normally found on aquatic vegetation, particularly water lilies, but is also often found on muddy bottoms in shallow water and the specimens from Lagoa Quilunda were mostly collected from wet flotsam along the water's edge on a beach of limestone shingle. *B. globosus* was found associated with all of the other species which occur in the same area except *Burnupia* sp. but it was most often found together with *Bulinus forskali* and for this reason its absence from Lagoa Cabemba is interesting.

SHELL (Pl. 9, figs. 1-5). Medium to large, globose, spire not pronounced but in older specimens the body whorl descends considerably relative to the penultimate whorl, aperture roughly oval, outer lip meeting the body whorl usually nearly at a right angle, columella truncate but the truncation sometimes poorly defined, callosity a little lighter in colour than the shell, columellar margin reflexed either completely to the body whorl or leaving a narrow umbilical slit. The colour is usually pale yellowish-brown but sometimes darker; clean shells are shiny and the sculpture consists of fine growth lines, occasionally with a more marked pattern of fine wavy lines.

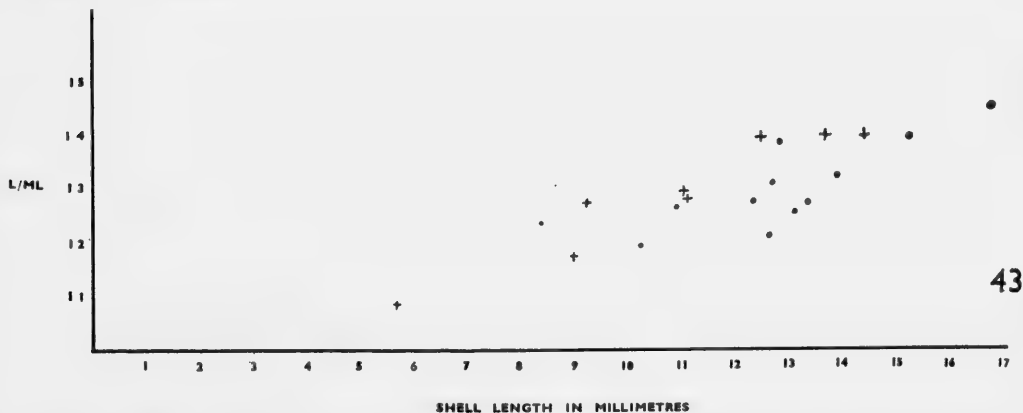


FIG. 43. Mean value of the ratio shell length/aperture length plotted against mean shell length for population samples of *Bulinus globosus* (*) and *B. africanus* (†).

The following table gives some of the dimensions in millimetres of a number of samples and Text-fig. 43 shows the mean value of the ratio shell length/aperture length plotted against mean shell length for populations of this species and of *B. africanus*.

Locality	Mean Length (Range in Brackets)	Mean Width	Mean Value l/ml (Range in Brackets)
Tentativa 1	13.1 (6.9-15.5)	10.1	1.25 (1.13-1.37)
Tentativa 2	10.9 (8.8-12.3)	8.4	1.26 (1.12-1.37)
Matoz	12.7 (4.3-16.6)	9.8	1.30 (1.17-1.44)
Libongo	16.8 (15.2-19.4)	10.6	1.45 (1.37-1.55)
Dalagosa	12.3 (6.0-18.0)	8.9	1.27 (1.06-1.46)
Bom Jesus	8.3 (4.0-16.2)	6.5	1.23 (1.13-1.41)
Quequesse	15.2 (12.8-18.4)	10.6	1.39 (1.35-1.45)
Cabungabunga	10.2 (7.1-15.5)	7.3	1.19 (1.10-1.37)
Quilunda	12.3 (5.75-15.7)	9.1	1.27 (1.06-1.42)
Lalama	13.9 (10.1-16.0)	10.7	1.32 (1.21-1.41)
Moembege	13.3 (11.7-14.4)	9.5	1.27 (1.20-1.34)
Quissol	12.6 (9.7-14.4)	9.1	1.21 (1.07-1.33)
Quionqua	12.8 (10.4-13.9)	8.9	1.38 (1.18-1.49)

ANATOMY. The mantle in fully grown specimens is usually uniformly black with a grey edge but in younger individuals it is pale grey with large black blotches. These pigmented patches increase in size until they coalesce and cover the whole mantle surface. The renal ridge on the underside of the mantle is almost always present in some form ; it may appear as a distinct crest running the length of the kidney or it may extend for only a short distance as no more than a slightly thickened median ridge. The intermediate ridge is well developed and roughly as long as the kidney.

The male copulatory organ is large, its length increases with shell length and the ratio of the length of penis sheath to that of preputium remains roughly constant at all growth stages. The mean value of this ratio in 147 specimens dissected from Lagoa Dalagosa is 0.83 and the range is from 0.56-1.50. The maximum width of the sheath is always less than that of the preputium and occurs as a regular dilatation near to the proximal end (Text-figs. 45-48, 50, 51). The preputium is darkly pigmented distally but the dark colour does not usually extend up to the junction with the sheath. The prostate grows steadily with increase in shell size up to a shell length of about 13 mm. and then the rate decreases but the accessory female glands appear to develop rapidly at a shell length of about 12 or 13 mm. The vagina is of medium length and the receptaculum seminis is globose in recently matured forms and about equal in diameter to the length of its duct (Text-figs. 44, 49). In older specimens the receptaculum becomes very distorted by the pressure of the accessory female glands.

Of the 147 specimens dissected from the Dalagosa population 36 per cent. were found to be infected by larval trematodes. The infection rate was highest in the larger size groups but this is probably due to immature infections in younger individuals being overlooked. The state of preservation of the material did not permit a detailed study of the larvae.

RADULA. There are six to eight tricuspid laterals in each half row, three or four transitional teeth and about twenty marginals. The cusps on the laterals are roughly triangular, broad-based and of medium length (Text-fig. 52). The endo- and mesocones are of approximately equal length and the ectocone is normally

about two-thirds the length of the mesocone. Aberrations are particularly common amongst the coastal plain populations, interstitial cusps in the centrals and on either side of the mesocone in the laterals are frequently found (Text-fig. 53), also sub-division of the endocone in all of the laterals. Another common aberration is a corrugation of the inner margin of the endocone on the inner laterals. Very small accessory cusps above either the endo- or ectocones are seen but are not as common as they are in *B. forskali*.

The type-locality for *B. globosus* is lakes on the banks of the Rio Dande, Angola. In Welwitsch's day the flood plain of the Dande must have been rather similar to that of the Cuanza at the present time with large, shallow lakes covering considerable areas during the dry season and joining to make an almost continuous stretch of water during the rains. Now however, the Mabubas dam which supplies Luanda with hydro-electric power has been thrown across the river above Caxito and the former flood plain below the dam is largely occupied by the sugar plantations of the Fazenda Tentativa. The "type habitat" of *B. globosus* therefore no longer exists but the species is common in the irrigation system of the plantation and in the stream which flows past the sugar refinery. Specimens from these places compare well with those in the type series (Pl. 5, figs. 6, 7) but none of the partially umbilicate forms (of which there are some specimens in the original series (Wright 1957)) was found. Morelet mentions that the species was also obtained by Welwitsch from the area of Moembege in the Cazengo district and it is possible that the aberrant specimens may have come from there and been mixed with the material from the Dande.

Both Connolly (1928) and Wright (1957) remarked on the poor development of the characteristic microsculpture of this species-group in Angolan specimens and this observation is confirmed by examination of further material. It is only well marked in a few young individuals and does not seem to persist on the later whorls as in material from Sierra Leone and other West African territories.

Carvalho and Janz (1960) record *B. globosus* from the drainage systems of the Zaire (Congo), Cuanza, Zambesie, Catumbela and Cunene (at Nova Lisboa). The samples on which their description is based are not large but they remark on (and figure) a considerable range of variation in the radula teeth and the constancy of the penis-sheath being shorter and narrower than the preputium. They remark on the absence of the species in many places in the east where the soil is sandy and the waters clean and note that it prefers stagnant water with decomposing organic material.

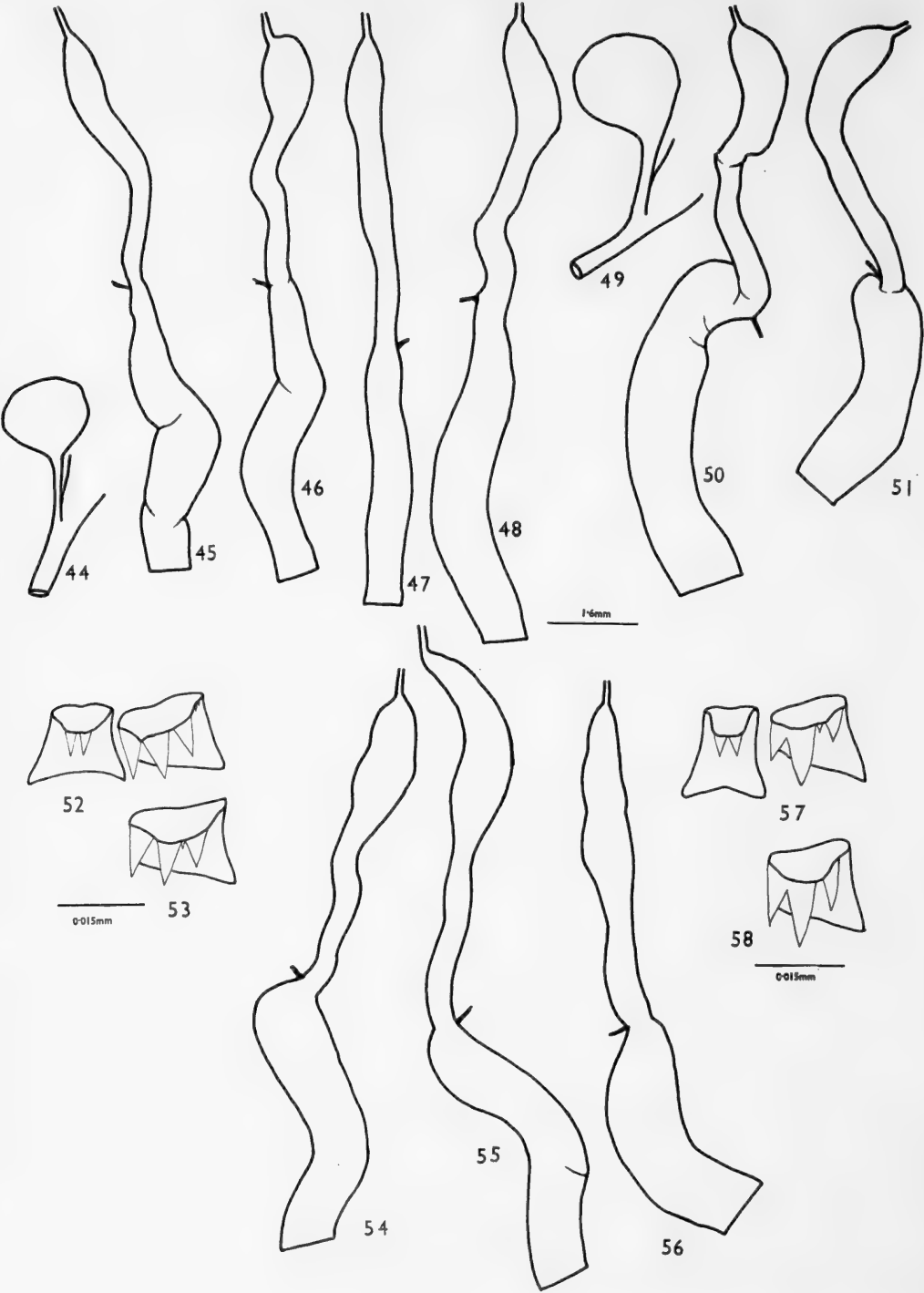
***Bulinus africanus* (Krauss)**

Physopsis africana Krauss, 1848: p. 85, pl. 5, fig. 14.

MATERIAL

Cangombe, Huila Province, pools in stream bed. 15 specimens. 21st November, 1957.

Capembe and San Jose, Huila Province, seepage ditch. 9 specimens. 21st November, 1957.



- Cassinde Pequeno, Huila Province*, small pools formed by surplus water from an open well. 34 specimens. 21st November, 1957.
- Cassinga, Huila Province*, backwater in Rio Cului. 3 specimens. 22nd November, 1957.
- Cativa, Huila Province*, washing place in Rio Cuando. 10 specimens. 23rd November, 1957.
- Cului (Rio), Huila Province*, bridge on Vila Artur de Paiva-Dongo road. 2 specimens. 23rd November, 1957.
- Dongo, Huila Province*, pools on margin of Rio Cubangue. 9 specimens. 23rd November, 1957.
- Gunda Vunjanga, Huila Province*, deep pool in stream bed. 7 specimens. 22nd November, 1957.
- Quesso, Huila Province*, two localities. (1) Irrigation system of Granja Administrativa. 7 specimens; (2) Marshy ground behind raised bank of Rio Cubango near washing place. 18 specimens. 21st November, 1957.
- Senga, Huila Province*, washing place in stream. 2 specimens. 22nd November, 1957.
- Vila Artur de Paiva, Huila Province*, ditch carrying surplus water from spring at main water point in town. 22 specimens. 21st November, 1957.

HABITAT. *Bulinus africanus* was found in nearly all of the localities visited in the neighbourhood of Vila Artur de Paiva in Huila Province. At the time when collections were made the rains were just beginning and water levels were low but all of the habitats were either in flowing water or pools in stream beds or ditches which would flow when the rains are at their height. In some places such as the seepage ditch at Capemba and San Jose and at Cassinde Pequeno the snails were collected in trickles of water so shallow that the shells were not fully covered but in most places they were found on aquatic vegetation.

SHELL (Pl. 4, figs. 6-8). The general appearance of the shell is similar to that of *B. globosus* but the outline is more ovoid, the spire is usually exerted and pointed, the aperture is more pronounced and the callosity is often whiter. The reflection of the columellar margin is similar to that in *B. globosus* in that there may be a narrow umbilical slit or it may be totally occluded.

The table gives some of the mean dimensions of the larger samples from populations studied.

FIGS. 44-53. *Bulinus globosus*. Figs. 44 & 49 receptacula and Figs. 45-48 male copulatory organs of specimens from Lagoa Dalagosa. Fig. 50. Male copulatory organ of specimen from Fazenda Libongo. Fig. 51. Male copulatory organ of specimen from Fazenda Tentativa. Figs. 52 & 53. Radula teeth.

FIGS. 54-58. *Bulinus africanus*. Figs. 54-56. Male copulatory organs of specimens from Cassinde Pequeno. Figs. 57 & 58. Radula teeth.

Locality	Mean Length	Mean Width	Mean Ratio Shell Length/ Aperture Length
Casinde Pequeno	13 (11.3-16.8)	8.7	1.39 (1.23-1.51)
Cangombe	14.4 (8.8-18.0)	9.2	1.39 (1.13-1.72)
Queso 2	12.5 (10.2-14.8)	7.95	1.39 (1.15-1.53)
Cativa	9.1 (3.2-20.0)	6.3	1.22 (1.05-1.45)
Vila Artur de Paiva	11.0 (6.5-16.8)	7.8	1.28 (1.11-1.48)
Dongo	5.7 (3.5-8.0)	4.5	1.08 (1.05-1.11)

The mean values of shell length/aperture length are plotted against mean shell length together with those for *B. globosus* in Fig. 43 and it can be seen that the values of this ratio in *B. africanus* from Huila tend to be rather higher at any given shell length than those for *B. globosus*, an expression of the greater exertion of the spire in the present species.

On young, clean shells of *africanus* the micro-sculpture of fine wavy lines is usually more clearly marked than in the lowland *globosus*.

ANATOMY. The only anatomical character in which Angolan *B. africanus* has been found to differ from *B. globosus* is the male copulatory organ. The mean ratio of penis-sheath/preputium in 32 specimens from three of the populations examined is 1.04 with a range from 0.8-1.4. The maximum diameter of the sheath in *africanus* is about $\frac{1}{2}$ of its length from the proximal end and it does not occur as a smoothly regular dilatation as in *globosus* but as a rather irregular widening (Text-figs. 54-56). The preputium is usually marked with alternating bands of light and dark pigment.

RADULA. There are six to seven tricuspid laterals, three or four transitional teeth and about twenty marginals in each half row. The centrals tend to be narrower and slightly longer-cusped than those in *globosus* and the mesocones of the laterals are usually distinctly longer and more dagger-like. The endocones of the laterals are about two-thirds as long as the mesocones while the ectocones are only about one-third as long (Text-figs. 57, 58). There is often a slightly greater degree of fusion of the bases of the endo- and mesocones in *africanus* than there is in *globosus*. Aberrations similar to those in *globosus* have been seen in this species but are by no means so common.

Bulinus africanus was described by Krauss from material collected near Durban. According to Mandahl-Barth (1957b) its distribution is confined to Natal, Transvaal, Northern and Southern Rhodesia and probably also Mozambique and Southern Tanganyika. The present material does not agree in detail with Mandahl-Barth's description of *africanus*, particularly with respect to the proportions of the male copulatory organ. Mandahl-Barth illustrates the penis-sheath as being almost twice as long as the preputium and slightly wider but the material from Huila has the two parts of the organ more nearly equal to one another both in length and diameter. The cusps of the lateral radula teeth are certainly larger than those of *globosus* from the type-locality but there is no great difference in the size of the teeth themselves.

The shell characters are closer to *africanus* than *globosus*. The smaller angle at the upper end of the aperture was a character used by Pilsbry and Bequaert (1927) to distinguish *B. africanus* from the form which they considered to be its sub-species *B. a. globosus*. Mandahl-Barth (1957b) emphasizes the distinctness of the columellar truncation and its frequent accentuation by a strong white callosity in *africanus* but Connolly's (1939) criterion of the complete absence of an umbilical slit in *africanus* does not appear to be valid.

The occurrence of *B. africanus* in the southern upland region of Angola not associated with the very closely related *B. globosus* from the northern plateau and coastal plain is extremely interesting. The different distributions of the two species may be due to different ecological requirements but in view of their apparent sympatric distribution in south-east Africa this seems unlikely. It is more probable that the two species are derived from different geographical origins. In a discussion of taxonomic problems in *Bulinus* Wright (1961) mentioned the possibility that the *africanus* species-group had its origin somewhere in the Tanganyika region and that the species within the complex are no more than the terminal parts of clines radiating from this centre. It is significant that *B. africanus* is most clearly distinct in the eastern part of the Union of South Africa and that the drainage from the southern part of the Angolan plateau is connected with this region through the Okavango swamp in Bechuanaland. This suggests that *B. africanus* may have reached Angola by this route while *B. globosus* has spread by the more direct line from Tanganyika through Northern Rhodesia and Katanga to the northern part of the plateau and the coastal plain. According to Carvalho and Janz (1960) there are large areas in the extreme eastern part of Angola where no snails of the *africanus* group are found, due to unfavourable ecological conditions. This area may have served as a barrier to direct westward movement and forced a separation into the northern and southern routes suggested above.

Bulinus angolensis (Morelet)*

* On line-priority the name used for this species should be *B. welwitschi* but the name *angolensis* is better known and, since it is inevitable that further work on this complex in other parts of Africa will reveal facts necessitating further nomenclatorial changes, the more commonly used name has been retained to avoid unnecessary confusion.

Physa welwitschi Morelet, 1866: p. 162. Morelet, 1868: p. 88, pl. 9, fig. 9.

Physa angolensis Morelet, 1866: p. 162. Morelet, 1868: p. 88, pl. 9, fig. 8.

Physa parietalis Mousson, 1887: p. 298, pl. 8, figs. 8 and 8a.

Bulinus tropicus angolensis; Carvalho & Janz, 1960.

MATERIAL

Catoco, Huila Province. Pools in stream bed. 78 specimens. 21st November, 1957.

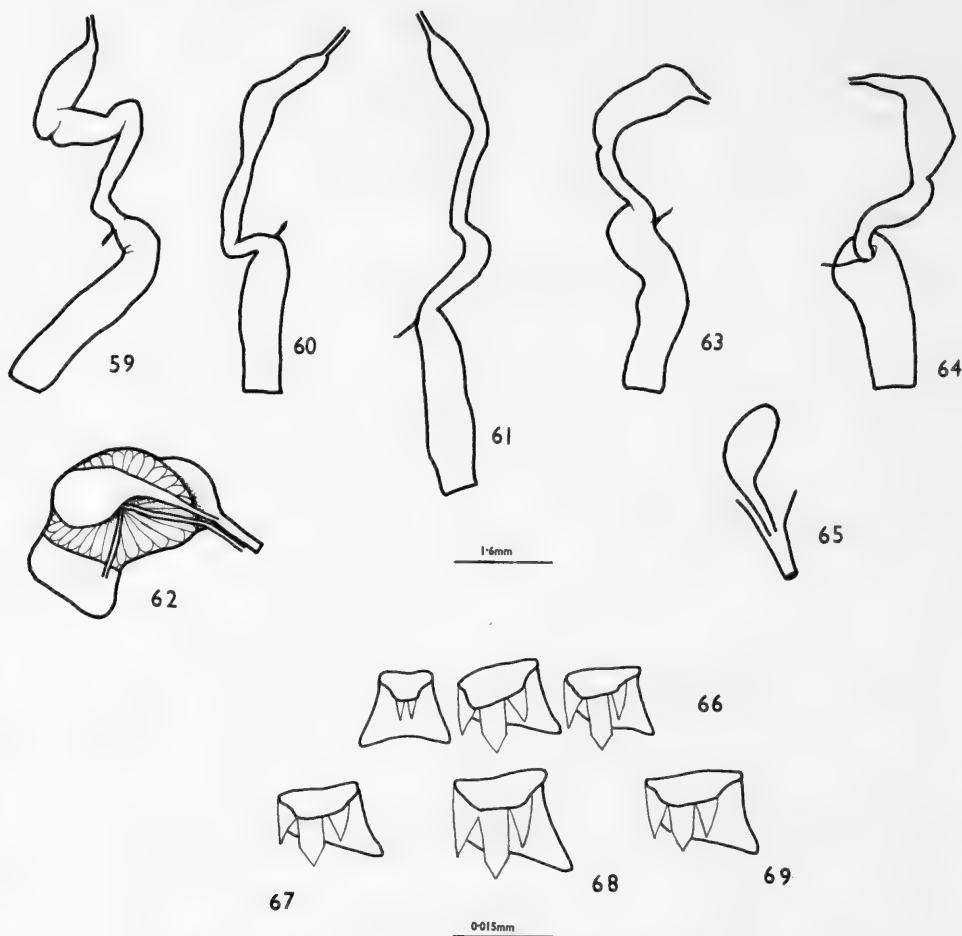
Cangombe, Huila Province. Pools in stream bed. 3 specimens. 21st November, 1957.

Cului (Rio), Huila Province. 9 specimens. 23rd November, 1957.

Dongo, Huila Province. Pools on margin of Rio Cubangue. 28 specimens. 23rd November, 1957.

Senga, Huila Province. Washing place in stream. 4 specimens. 22nd November, 1957.

Quissol (2) (Fazenda). Pool in Quastimbala stream, near Malange. 14 specimens. 23rd October, 1957.



FIGS. 59-69. *Bulinus angolensis*. Figs. 59-61. Male copulatory organs of specimens from Dongo. Fig. 62. Receptaculum and prostate of specimen from Dongo. Figs. 63 & 64. Male copulatory organs of specimen from Quissol. Fig. 65. Receptaculum of young specimen from Quissol. Fig. 66. Radula teeth of specimen from Quissol. Fig. 67. First lateral radula tooth of specimen from Catoco. Fig. 68. First lateral radula tooth of syntype of *Bulinus welwitschi*. Fig. 69. First lateral radula tooth of syntype of *Bulinus angolensis*.

HABITAT. All of the localities from which this species was collected were either gently flowing streams or pools in stream beds. The snails were always found on aquatic vegetation and never on the mud.

SHELL (Pl. 5, figs. 1-5). The shell in this species is very variable. It ranges from globose with a depressed spire to ovoid or almost oblong with a well developed spire. In large specimens the upper whorls are regularly ribbed while the later ones have only irregular growth lines but in small individuals the whole shell is regularly ribbed. The colour varies from light reddish-brown to almost colourless. The aperture is ovate in globose specimens with the outer margin regularly curved but in higher spired forms the outer lip is often flattened and almost straight. The columella is sometimes slightly twisted and the reflection of the columellar margin varies but all of the specimens examined were narrowly umbilicate. The following are the mean lengths together with the ratio shell length/aperture length of several of the populations examined :—

Locality	Length	Shell Length Aperture length
Catoco	9.15 (3.7-11.2)	1.27 (1.09-1.58)
Dongo	5.4 (2.72-7.8)	1.15 (1.04-1.26)
Cangombe	11.7 (11.2-12.8)	1.37 (1.32-1.45)
Quissol	5.5 (4.0-9.6)	1.17 (1.08-1.33)

ANATOMY. The mantle varies from almost white to light grey with regular, large black spots, often roughly circular. The intermediate mantle ridge varies in length between half and one-third that of the kidney. The male copulatory organ is variable in size and in the proportions of the penis-sheath and preputium. In the sample from Quissol five of the ten specimens dissected were aphyallic and the sheath was longer than the preputium in those individuals with a copulatory organ (Text-figs. 63, 64), the maximum diameters of the two parts were approximately equal. The receptaculum seminis is clavate, its long axis is about equal in length to its duct which is in turn equal to the length of the vagina (Text-fig. 65). The samples from the southern part of the plateau show considerable variation in both the occurrence and proportions of the male copulatory organ. From Catoco two out of the seven dissected were aphyallic and the sheath/preputium ratios in the others varied between about 2 : 1 and 3 : 2 (Text-figs. 59, 60). From Dongo two out of ten were aphyallic and the proportions of the parts in the euphallic individuals ranged between about 3 : 1 and 2 : 1 (Text-fig. 61) while from the Rio Cului the five largest specimens (ranging in shell length from 4.0-4.8 mm.) were dissected and all were found to be aphyallic. No aphyallic individuals occurred in the two small samples from Senga and Cangombe and the proportions of the parts of the male organ varied between 3 : 2 and 5 : 3. Two of the three specimens from Cangombe were grossly infected with larval trematodes but no cercariae were found in a sufficiently good state of preservation to enable an identification to be made. One of the snails from Dongo was heavily infected with larval amphistome flukes.

RADULA. There are five to seven tricuspid laterals in each half-row and up to twenty marginals. The teeth are smaller than those in *B. globosus* and larger than those in *B. truncatus rohlfsi* but they are similar to those in *rohlfsi* in that the mesocone of at least the first lateral and often all of the laterals has the arrow-head

shaped tip characteristic of the *truncatus* species group (Text-figs. 66, 67). Aberrations in the form of the teeth are fairly common, particularly an assymetrical development of the central and sub-division of the endocones of the laterals.

The material which has been available for this study is inadequate to assess properly the relationships of the species or even to make a proper description of its probable full range of variation. The most important fact which has emerged is the apparent relationship of *angolensis* to the *truncatus* group rather than to the *tropicus* complex to which it has so far been referred.

None of the specimens examined is conchologically close either to the type series of *angolensis* (Pl. 6, figs. 4, 5) or to that of *welwitschi* (Pl. 6, figs. 1-3) but many of the specimens from the southern plateau region resemble the illustration of Mousson's *parietalis*. Mandahl-Barth (1957b) tentatively refers *parietalis* to the synonymy of *angolensis* but he points out that it is not possible to be definite about this until material from the type locality of *parietalis* at Ondangua in Ovamboland (near the border between Angola and South-west Africa) is available. However, in a footnote on page 60 of his monograph (1958) he refers to material of *Bulinus truncatus* from Ondangua and the photograph of one of these specimens in a later paper by the same author (1960) shows it to be very like the types of *angolensis*. In the same paper Mandahl-Barth also illustrates a specimen of *B. truncatus* from Kalambo in the Congo and this shell, although larger, is similar to the largest specimen in my sample from Quissol. Bequaert and Clench (1933) recorded two dead specimens of *B. angolensis* from the Inkisi river near Kisantu, also in the lower Congo area. The type locality for *angolensis* is said to be in the district of Duque de Braganza towards the northern end of the plateau but Welwitsch himself was unable to reach this area and his manuscript notes on the specimens sent to Morelet contain a supplement mentioning several samples from this region which were collected by a friend in 1862-3 after Welwitsch had left Angola and in no case is the origin of the samples more clearly defined than by reference to the district. During the present expedition a number of localities in the Duque de Braganza area were searched but the only specimens found were those from Quissol, just south of Malange. The type locality for *welwitschi* is near the Bumbo river in the south of Angola in the Mossamedes area.

One of the syntype specimens of *angolensis* and two of the type series of *welwitschi* were found to contain dried remains of the original animals. By incubation for an hour at 28° C. in a 2 per cent. solution of tri-basic sodium phosphate (after the method of Van Cleave and Ross, 1947) the bodies were sufficiently soft to be removed from the shells. They were left for three days in 0.5 per cent. tri-basic sodium phosphate at room temperature and then dissected. The tissues were very brittle and accurate measurements of the male copulatory organs were not possible but that of *angolensis* had an approximate sheath/preputium ratio of 2 : 1 and one of the *welwitschi* was aphallic while the other had a penis complex similar to that of *angolensis*. The euphallic specimen of *welwitschi* was infected with amphistome cercariae apparently similar to those found in one of my specimens from Dongo. Preparations of the radulae from these three paratype specimens (Text-figs. 86, 69)

showed them to be similar to those described from the recent material and all of them have the arrow-head shaped mesocone of the first lateral.

Carvalho and Janz (1960) have followed the usage of Mandahl-Barth and refer to *angolensis* as a sub-species of *B. tropicus*. They have studied specimens from a number of localities and have found them to be widely variable. A large sample from Tchivinguiro near Sa da Bandeira was unlike any of the others in that the shells were high spired with acute apices and for this sample of 165 specimens the authors worked out the ratio of aperture length/shell length for all of the specimens. The ratio plotted as a frequency distribution gives a normal Gaussian curve with its lowest value at 0.3 and its highest at 0.7 with the median at 0.483. This emphasizes very strongly the enormous variation in shell shape within a population of this species. In the general anatomical description Carvalho and Janz make no mention of finding aphyallic specimens and they illustrate an aberrant individual with two penis sheaths and only a single preputium. The radula is not mentioned in the text but a figure of the central and first lateral of a specimen from the Tchivinguiro sample shows the mesocone of the lateral to be a simple conical cusp.

The distinctions between the *truncatus* and *tropicus* groups are not as clear-cut as has been suggested in the past and study of this Angolan material has led to an investigation of the two main distinguishing characters in some other material. Mandahl-Barth (1957b) records aphyallic specimens of *tropicus* in Northern Rhodesia but these may be an extension of the range of *angolensis*. The form of the mesocone of the lateral radula teeth cannot be regarded as diagnostic for the radulae of the paratypes of *B. tropicus* and *B. diaphana* in the Piele collection both have the mesocone cusp as arrow-head shaped as it is in such species as *B. truncatus rohlfsi* and *B. sericinus*. Only examination of a great deal more material will indicate whether *B. angolensis* is truly a member of the *truncatus* group or an aberrant *tropicus* or if it is genuinely a connecting link between the two groups.

***Bulinus truncatus rohlfsi* (Clessin)**

Physa rohlfsi Clessin, 1886: p. 349, pl. 49, fig. 7.

Bulinus truncatus rohlfsi; Mandahl-Barth, 1957(b).

MATERIAL

Panguila (Lagoa), north-west corner of lake near the mouth of the Rio Bengo.
8 specimens. 9th November, 1957.

Cabemba (Lagoa), large lake on flood plain of Rio Cuanza. About 150 specimens.
14th November, 1957.

HABITAT. In both localities this species was found associated with *B. forskali* on *Ceratophyllum* at all levels in water to a depth of about three feet near the lake shore and in Lagoa Cabemba on an open shore exposed to gentle wave action.

SHELL (Pl. II, figs. 8-19). Almost rectangular in outline with a low spire and smoothly rounded whorls. The outer lip of the aperture is nearly straight and only slightly curved, it meets the body whorl almost at right angles. The columella is more or less straight and the columellar margin is reflexed so that the umbilicus



FIGS. 70-76. *Bulinus truncatus rohlfsi*. Figs. 70 & 71. Heavily marked and lightly marked mantles. Figs. 72 & 73. Male copulatory organ and receptaculum of laboratory-bred specimen from Lagoa Cabemba stock (7.3 mm. shell-length). Figs. 74 & 75. Accessory genital glands and male copulatory organ of wild specimen from Lagoa Cabemba (5.1 mm. shell-length). Fig. 76. Radula teeth.

is closed. The specimens from Panguila are white and shiny while those from Cabemba are shiny, translucent and almost colourless. The sculpture consists of regular poorly developed ribs mostly on the upper whorls while on the body whorl there are usually only fine growth lines. The longest specimens in both samples were 6.4 mm. long, 5 mm. wide, 5.2 mm. aperture length and 3.2 mm. aperture width and the majority fell within the 4-5 mm. shell length range.

ANATOMY. The mantle pigmentation varies from a number of dark grey or black blotches, particularly in the area overlying the kidney, with a series of smaller black markings inside the mantle border, to completely white and all intermediate forms occur (Text-figs. 70, 71). The intermediate ridge between the kidney and rectum is short, not more than half the length of the kidney and seldom more than a third as long.

All of the specimens from *Panguila* were dissected and found to be aphyallic and only eight out of forty of those examined from Cabemba had a fully developed male genital system. The copulatory organ, when present, is large, roughly 5 mm. long in a specimen of 6 mm. shell-length. The penis sheath and preputium are roughly equal in length but the sheath is sometimes a little longer (Text-figs. 72, 75). The proximal dilatation of the sheath is about equal in diameter to the preputium and it occupies about a third of the length of the sheath. The penis is large and folded within the dilated part of the sheath which is often transparent and the epiphallus is about half to two-thirds the length of the sheath. The development of the rest of the male genital system is variable, in aphyallic specimens there may be no trace of sperm duct, prostate or vas deferens while in others there may be a relatively well developed sperm duct and a rudimentary prostate. Even in euphyallic individuals the prostate never attains the relatively large size that it reaches in members of the *forskali* and *africanus* species complexes. The sperm duct in normal specimens is about twice the diameter of the vas deferens and is moderately convoluted; in aphyallic individuals the sperm duct, if present, is narrower and almost straight. The seminal vesicle has small tuberculate projections and is situated near the distal end of the hermaphrodite duct, about one third of the duct length from the carrefour. The translucent funnel beneath the ovotestis at the proximal end of the hermaphrodite duct is rather longer than in most bulinids, approximately equal in length to one third of the duct.

The vagina is short and slightly bulbous, the receptaculum seminis duct opens into it near its junction with the uterus. The receptaculum is almost globular and its diameter is roughly equal to the length of its duct (Text-figs. 73, 74). The uterus and its associated glands are relatively large and the oviduct is wide and scarcely convoluted. The accessory female glands in aphyallic individuals appear to be fully developed and functional at a shell-length between 4.5 and 5.0 mm.

RADULA. There are 20–25 teeth in each half-row of the radula, five or six of which are tricuspid laterals. In a number of radulae from both *Panguila* and Cabemba small interstitial cusps were found to be present on either side of the mesocone in all of the laterals and sub-division of the endocone of even the first lateral was observed in several specimens. The mesocones of the laterals are relatively long and broad and arrow-head shaped at the tip (Text-fig. 76).

The status of the sub-species *B. truncatus rohlfsi* is still dubious and a great deal of work is needed to elucidate its relationships. The present material is referred to this sub-species with some reservations, particularly in the light of the finding that *B. angolensis* is also a member of the *truncatus* group. Comparison with specimens from Lake Barombe Mbo in the Cameroons shows no significant differences.

Material of *rohlfsi* from the neighbourhood of Ibadan in Nigeria has a higher spire and darker coloured shell. Both the Nigerian form and that from Lagoa Cabemba have been bred in the laboratory for over three years and the two cultures retain some of the distinctions that were apparent in the original stocks although the appearance of both forms has been modified by laboratory breeding conditions. The changes which have occurred in the Angolan form are similar to those observed by Schwetz (1954) in a laboratory bred population of *Bulinus coulboisi* originating from Lake Tanganyika and the resemblance in shell-form between the wild stocks of both Schwetz's material and that from Cabemba is very marked. Mandahl-Barth (1957b) comments on the extremely close similarity between *B. coulboisi* and *B. trigonus* apart from the characters of the radula teeth which have simple triangular mesocones on the laterals in *coulboisi* but arrow-head shaped cusps in *trigonus*. On these grounds the present material is in many respects similar to *trigonus* and the question of the relationships between the lake forms of the *truncatus* group and the more widely distributed *rohlfsi*-like forms merits investigation. This point is further emphasized by Mandahl-Barth's (1960) remarks on the conchological similarity between specimens of *B. truncatus* (now referred to *B. angolensis*) from Ovamboland and *B. transversalis* from Lake Victoria.

Larambergue (1939) showed that the apthallic condition in *Bulinus truncatus* is a genetically controlled character and that the proportion of apthallic to eupthallic individuals in a population is a more or less constant character. He also demonstrated that the degree of pigmentation of the mantle is genetically controlled and that the blotched form is dominant to the unmarked. Although no controlled experimental work has been carried out on the Angolan material the question of the simple dominance of the blotched mantle is questionable since by far the greater proportion of individuals examined have intermediate degrees of pigmentation and the number of heavily marked specimens only slightly exceeds the number of unmarked. One thing is certainly clear and that is the absence of linkage between mantle pigmentation and the condition of the male copulatory organ for both blotched and unmarked individuals have been found to be eupthallic.

Laboratory bred specimens of the material from Lake Cabemba have been successfully infected with *Schistosoma haematobium* from both Cairo and Khartoum. The Angolan snails appear to be as susceptible to infection as the "normal" hosts for each strain from the point of view of the proportion of exposed individuals which shed cercariae but they produced less cercariae and appeared to lose the infection after shedding more easily than the normal hosts. The cercariae from the Cabemba snails were infective to hamsters which subsequently passed viable eggs.

Bulinus forskali (Ehrenberg)

Isidora forskalii Ehrenberg, 1831: p. 20.

Bulinus schmidtii Dunker, 1853: p. 9, pl. 2, figs. 7, 8.

Physa capillacea Morelet, 1868: p. 89, pl. 8, fig. 1.

Physa apiculata Morelet, 1868: p. 90, pl. 8, fig. 3.

Physa semiplicata Morelet, 1868: p. 91.

Physa turriculata Morelet, 1868: p. 92, pl. 9, fig. 7.

Physa clavulata Morelet, 1868: p. 93, pl. 9, fig. 6.

Physa moreleti Nobre, 1905: p. 15, pl. 1, figs. 29, 30.

Physa osorioi Nobre, 1905: p. 15, pl. 1, figs. 31, 32.

MATERIAL

Bom Jesus, small lake on banks of Rio Cuanza. 17 specimens. 13th November, 1957.

Cabemba (Lagoa), large lake on flood plain of Rio Cuanza. 8 specimens. 14th November, 1957.

Cabungabunga (Lagoa), large lake on flood plain of Rio Cuanza. 17 specimens. 13th November, 1957.

Dalagosa (Lagoa), lake on flood plain of Rio Cuanza. 66 specimens. 13th November, 1957.

Dondo, Rio Mucoso. 38 specimens. (Sample received from Dr. Morais de Carvalho). 3rd July, 1957.

Guimbe (Lagoa), large lake on flood plain of Rio Cuanza. 26 specimens. 13th November, 1957.

Lalama (Lagoa), lake near junction of Rio Calucala and Rio Bengo. 12 specimens. 14th November, 1957.

Lumango (Lagoa), lake near Rio Bengo. 1 specimen. 14th November, 1957.

Panguila (Lagoa), lake near the mouth of the Rio Bengo. 2 samples :—(a) pool on the bank near the south-west corner of the lake. 26 specimens. 8th November, 1957 ; (b) North-west corner of the lake itself. 100+ specimens. 9th November, 1957. Also laboratory-bred material from the same stock.

Quilunda (Lagoa), large lake on the banks of the Rio Bengo. 40 specimens. 14th November, 1957.

Fazenda Tentativa, irrigation ditches on sugar plantation. Not many specimens collected but laboratory-reared material examined.

Matoz (Lagoa), small lake on the edge of the Fazenda Tentativa, on the Rio Dande drainage. Specimens collected from a small seepage ditch beside the lake. 10 specimens. 8th November, 1957.

Cuije (Rio), small pool on flood plain of the river. 5 specimens. 24th October, 1957.

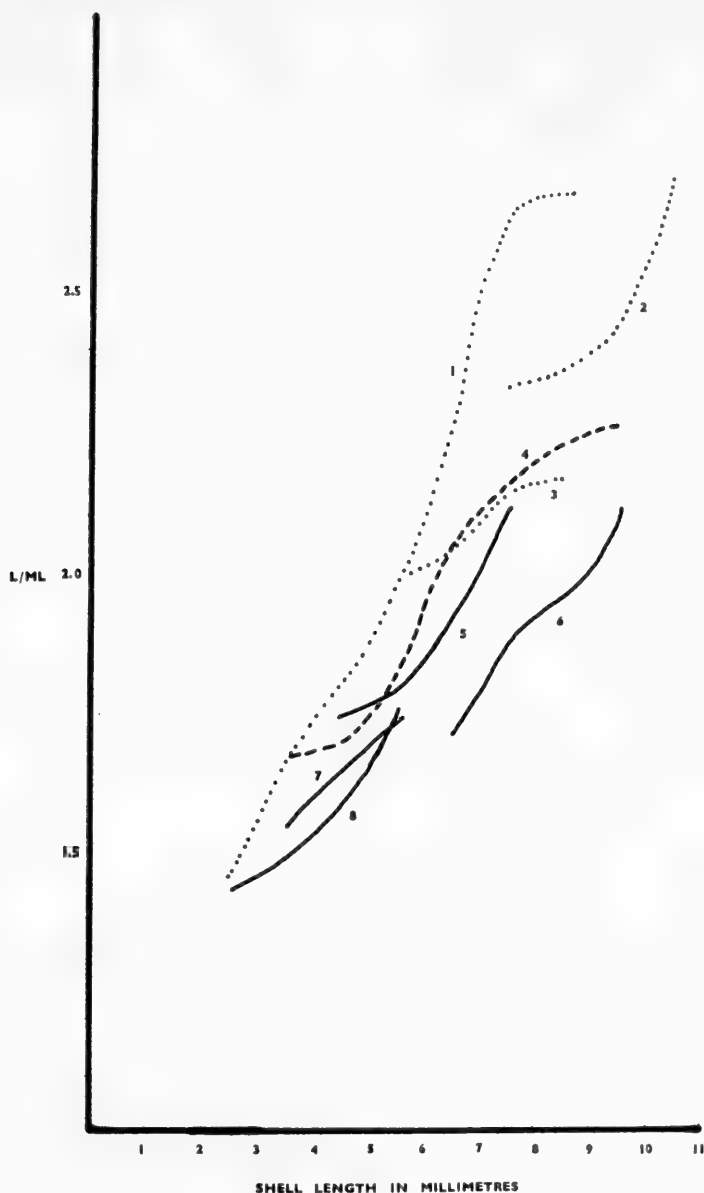
Quionqua (2), small pool beside road. 4 specimens. 25th October, 1957.

HABITAT. The habitat of the material from Dondo is unknown. All of the other localities on the Cuanza flood plain are basically similar and the snails were either collected from the under side of waterlily leaves or from amongst *Ceratophyllum* which was present in most of the lakes. The habitat in Lagoa Panguila was similar and the specimens from the pool on the banks of the lake were collected from emergent grass. The material from Lagoas Lumango and Lalama was found in the wide surrounding reed bed which was present in both of these lakes. Lagoa Quilunda is unique amongst the lakes visited in that it apparently contains little aquatic plant life and has a stony bottom and beach with occasional tufts of emergent grasses. The snails were found on the grass or among debris washed-up along the

water's edge. The material from Lagoa Matoz was found in a shallow (4-6") seepage ditch beside the lake. The pool on the flood plain of the Rio Cuije was about four feet across and only 4-5" deep with full sun exposure, almost certainly a temporary pool, and that near Quionqua was about three feet deep, slightly shaded, with a thick mud bottom and rotting vegetation; the snails were found on emergent grasses in both places.

SHELL (Pl. 8, figs 1-16). There is a great range of variation in shell-form within this species but there are certain more or less constant characters. The upper whorls are nearly always ribbed and carinate, the carination forming a well-defined shoulder on the upper part of the whorl. The exertion of the spire is a slightly variable character. The specimens from Dondo have strongly ribbed and shouldered upper whorls but the body whorl is often smoother and lacks the carination. The other samples from the Cuanza flood plain (Bom Jesus, Cabemba, Cabungabunga, Dalagosa and Guimbe) are very similar to one another. The shells are yellowish, thin, strongly ribbed and shouldered and, where the ribs join the shoulder the periostracum is produced into quite well-marked spines. The material from Panguila is similar but the shells are mostly colourless, the carination is not so well-marked and in many the spiral punctate pattern of the embryonic shell is continued on to the second and third whorls becoming modified into a faint spiral sculpture superimposed on the ribbing. In the sample from Quilunda the shells are thicker than any of the others, colourless and transparent and some are strongly ribbed and carinate while others are smoother and scarcely shouldered. The material from Lalama and Matoz is similar in the variability of the shouldering and that from Fazenda Tentativa (laboratory bred) shows few shouldered specimens although all are quite strongly ribbed. The few individuals from the pool near the Rio Cuije are well ribbed and shouldered on the upper whorls but all the specimens show a dark band (probably the remains of a peristome formed during aestivation) and below this band there is scarcely a trace of either ribbing or carination. The specimens from Quionqua are all ribbed and shouldered and two of them show small shoulder spines.

Variation in the degree of exertion of the spire in different populations is well shown in Text-fig. 77 in which the mean values of the ratio shell length/aperture length are plotted against shell length. A number of interesting points are illustrated by this graph. First, the populations from the flood plain of the Rio Cuanza show a slightly lower ratio than those from around the Rio Bengo, indicating that they have a more squat appearance, second, there is an appreciable difference in the ratio between specimens from the pool on the banks of the Lagoa Panguila and those from the lake itself and lastly, the ratio is lower in specimens bred in the laboratory from the lake form than it is in the original wild sample. It can also be seen that the size range of the different samples varies considerably despite the fact that the collections (with the exception of the laboratory bred material from Panguila and the sample from Dondo) were all made within a period of a week. The following table gives the mean shell length and its range for some of the samples:

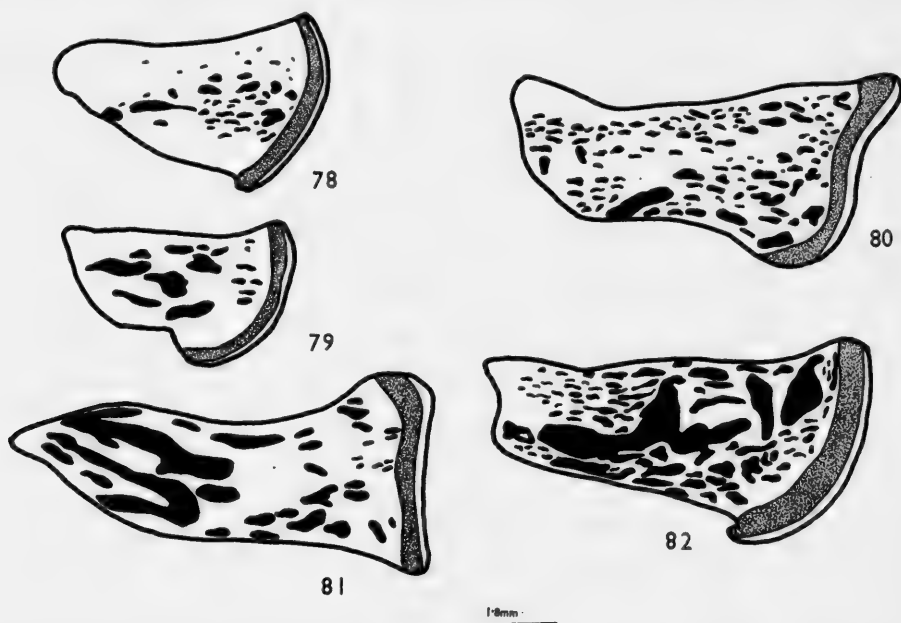


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FIG. 77. The ratio shell length/aperture length plotted against shell length for population samples of *Bulinus forskali*. 1. Lagoa Panguila, north end of lake. 2. Lagoa Panguila, pool on edge of lake. 3. Lagoa Panguila, laboratory bred. 4. Lagoa Quilunda. 5. Lagoa Cabungabunga. 6. Dondo. 7. Lagoa Guimbe. 8. Lagoa Dalagosa.

Locality	Maximum Length	Minimum Length	Mean
Bom Jesus	9.5	3.0	5.7
Cabemba	5.1	2.7	4.1
Cabungabunga	7.4	4.0	5.9
Dalagosa	6.1	2.5	4.1
Guimbe	5.1	3.0	4.0
Quilunda	9.8	3.0	5.9
Panguila (pool)	11.5	7.0	8.8
Panguila (lake)	7.0	2.2	4.2

These figures are of little value without some indication of the maturity of the population and this will be discussed under the anatomical part of this description.



FIGS. 78-82. *Bulinus forskali* mantles. Figs. 78 & 79. Lagoa Dalagosa. Figs. 80 & 81. Lagoa Quilunda. Fig. 82. Dondo.

ANATOMY. The markings of the mantle vary considerably between individuals of the same population but there are definite trends in the distribution of the pigment which are associated with other differences between populations. The basic pattern consists of a light grey ground colour with a fairly wide darker grey band near the margin and a light grey or creamy edge. In those forms with strongly ribbed and carinate shells there are usually fewer dark markings than in the less shouldered populations but in these smoother forms there may be less actual pigment present although it is more widely distributed (Text-figs. 78-82). In the forms with a few dark markings the pigment is usually concentrated over the kidney.

The male copulatory organ is also variable. The penis sheath is a little longer than the preputium, in most populations the proportion is roughly 4 : 3 or 3 : 2 but in the sample from Dondo it approached 2 : 1. The maximum diameter of the dilatation of the sheath is about equal to the diameter of the preputium and lies about a quarter to one third of the sheath length from its proximal end (Text-figs. 83-90). The epiphallus is always short, about one third of the length of the sheath.

The female genital system shows no characters of sufficient constancy to merit consideration from a taxonomic point of view. The appearance of the receptaculum seminis varies greatly according to the age of the individual but in recently mature specimens it is ovate and the length of the dilated part is a little longer than the duct.

The main interest in the genital anatomy of these snails is in determining the state of maturity of the specimens and from this trying to obtain some idea of the reproductive activity of the populations. In *Bulinus jousseaumei* Wright (1957) has shown that there is a connection between the development of the accessory genital glands and the increase in the ratio shell length/aperture length. It has also been shown (Wright 1960) that there is an increase in shell length in *B. forskali* associated with the onset of maturity. In both cases these relatively sudden changes in growth rate are necessary to provide a greater shell volume to accommodate the accessory genital glands. The development of these glands is protandrous, the prostate becomes clearly defined and apparently functional before the muciparous and oöthecal glands of the female system are properly differentiated. In the fully mature adult snail the total volume of the accessory female glands exceeds that of the prostate by about three times, but egg-laying may have started before this when the prostate is about half the size of the female glands. This is taken as a rough index of the attainment of reproductive maturity, and the observations reported here are based on this criterion. At shell length 3.0-3.5 mm. the snails from Dalagosa and Guimbe have fully developed prostates and are mature between 4.0 and 4.5 mm., while those from Cabungabunga and Bom Jesus do not reach maturity until they have attained a length of 7.0-8.0 mm. The largest specimen from Cabemba was 5.1 mm. long and showed no appreciable development of the female glands. These samples come from relatively close localities and were all collected in two days. The specimens from Dondo reach maturity at a length of 7.0-8.0 mm. as do those from Quilunda and Lalama. The sample from Panguila (lake) are mature at about 6.5-7.0 mm. The results fit well with those anticipated from the form of the curves in Text-fig. 77 and emphasize the dangers of using absolute shell length as a criterion of maturity in this species. Whether these effects are ecological or genetically controlled remains to be determined.

RADULA. Teeth from a typical radula are illustrated in Text-fig. 91. The majority of the specimens examined had six tricuspid laterals and about fifteen marginals but there is a good deal of variation in these numbers which is not necessarily related to the size of the snail (small individuals may have as many as nineteen marginals while larger specimens may have only twelve or thirteen). Nearly all

of the radulae examined showed small interstitial cusps between the main cusps of the laterals and the majority also had small accessory cusps on the inner margin of the endocone or on the outside of the ectocone. A large proportion of radulae with regularly malformed teeth were observed and these were more common in some populations than in others, the proportion of aberrant specimens being particularly high in the sample from Bom Jesus and some of these are illustrated in Text-figs. 92-95.

Bulinus forskali is well known as one of the most variable species of freshwater snail in Africa and this accounts for the large number of named species which have subsequently been shown to be extreme forms of *forskali*. The relatively long list of synonyms at the beginning of this description shows that the species is particularly variable in Angola. The names given by Morelet are convenient terms for referring to forms of the species because each of Morelet's "species" is based on an extreme development of particular characters. It is useless to think in terms of *B. forskali* from the Nile delta (the type locality) as being typical of the species but it is helpful to consider the dominant form in any region as being the most characteristic for that area. From a study of material collected during this expedition it is apparent that Morelet's *capillacea* (Pl. 7, figs. 4, 5) is the most commonly occurring form in Angola. All of the specimens from the Cuanza flood plain are very close to this form in their smaller size ranges, and the samples from Bom Jesus and Dondo clearly establish that *clavulata* (Pl. 7, figs. 11-14), *turriculata* (Pl. 7, fig. 10) and *schmidtii* (Pl. 7, figs. 1-3) are merely extreme developments of this basic form at larger sizes. The forms *apiculata* (Pl. 7, figs. 6-10) and *semiplicata* (Pl. 7, figs. 15-17) are simply growth stages of the poorly carinate variety, they occur in mixed populations with the *capillacea* type in Panguila, Quilunda, Lalama and Fazanda Tentativa where they show all stages of intergrading. An examination of the type localities recorded for Morelet's species shows that there is probably a frequent shift in the dominance of any one form in a particular place. For instance, the type locality of *capillacea* is Libongo on the Rio Lifune and it is also recorded from Lagoa Quifandongo near the Rio Bengo but not from the Cuanza area where it is now the dominant form. *B. apiculata* and *semiplicata* were both originally described from the Cuanza drainage where neither form was found during this investigation (Morelet's description of *semiplicata* gives the origin of the material as pools near Mopopo, Rio Caranxa, but Welwitsch's manuscript notes definitely say "Rio Cuanza"). Mandahl-Barth (1957b) refers to *schmidtii* as the form of *forskali* characteristic of the Angolan and Lower Congo region but this is not strictly true as *schmidtii* is more obese and less markedly carinate than the commonest form in the area (Pl. 7, figs. 1-3). It has not been possible to examine the original material of Nobre's species *moreleti* and *osorioi* and so no definite conclusions about the affinities of these forms can be reached. From the illustrations it appears that *moreleti* is one of the strongly ribbed and carinate forms while *osorioi* resembles *apiculata*.

Carvalho and Janz (1960) mention the wide distribution of *B. forskali* in Angola and state that it is normally found in the shallow water of lakes or small streams.

Bulinus scalaris (Dunker)

Physa scalaris Dunker, 1845: p. 164.

Bulinus scalaris Dunker, 1853: p. 8, pl. 2, figs. 5, 6.

Physa canescens Morelet, 1868: p. 90, pl. 9, fig. 3.

Physa benguelensis Sowerby, 1873: pl. 9, fig. 77.

MATERIAL. Three specimens only, collected in a pool, Quionqua (1), about fifty kilometres north-north west of Malange on the road to the Duque de Braganza falls. 25th October, 1957.

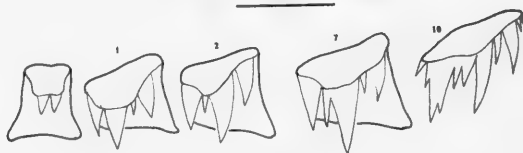
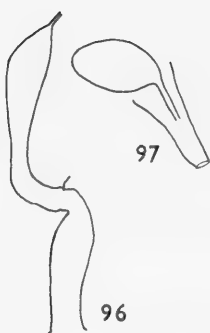
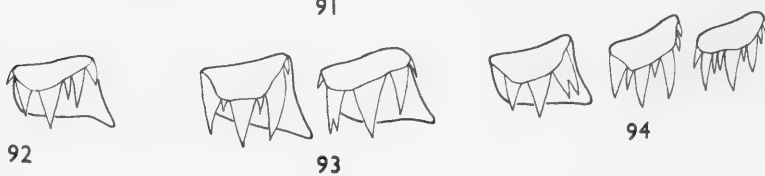
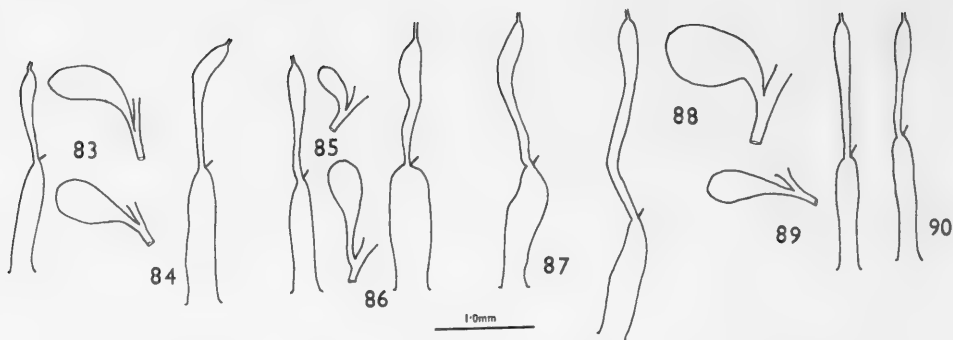
HABITAT. The pool was by the roadside, shallow and choked with grass, fully exposed to the sun and probably not permanent. At the time of the collection the rains had just begun and the pool appeared to have become only recently filled. *Bulinus globosus* was also found.

SHELL. All three specimens were large, the biggest was 11.1 mm. long, 4.9 mm. wide, 5.5 mm. aperture length and 2.7 mm. aperture width. The other two specimens were 9.7 mm. and 8.2 mm. long. The body whorl is approximately equal to half the length of the shell and, in the largest specimen the ratio of shell length/aperture length is only 2.02. The shells are thin and smooth on the lower whorls but the apical whorls are ribbed and slightly shouldered.

ANATOMY. All of the specimens were dissected and the penis was unfortunately everted in each. However, there was a considerable proximal dilatation of the penis sheath and all had a long epiphallus. In the two smaller individuals the prostate was about equal to half the total volume of the accessory genital glands, suggesting that both of the specimens were probably only just functionally hermaphrodite and not yet fully developed. The receptaculum seminis was ovoid and the duct was a little shorter than the maximum diameter of the receptaculum (Text-fig. 97). The mantle markings consist of large, irregular but separate black blotches on a pale grey ground with a wide band of darker grey near to the free edge (Text-fig. 98).

RADULA. The radula teeth are similar to those of *B. forskali* with slightly longer mesocones on the laterals. Very small interstitial cusps are present between the endo- and mesocones and between the ecto- and mesocones of all the laterals. The fourth lateral on one side of one of the radulae had an additional endocone. Each row had seven tricuspid laterals and sixteen marginals (Text-fig. 99).

It is interesting that this small sample was the only material of *B. scalaris* found during this investigation and it came from a locality well away from those previously recorded in Angola. The type-locality of the species given by Dunker is the marshy areas around lakes near Benguela. Sowerby gives the locality for *benguelensis* (Pl. 9, figs. 4-6) as Benguela, Egypt, but this almost certainly refers to the small coastal village of Egitto near Benguela. Morelet records *scalaris* from stagnant waters near Luanda and from *Lemna*-covered pools in the neighbourhood of Ambriz and gives the type-locality for *canescens* (Pl. 9, figs. 7, 8) as the marshes around the river Bengo near Quicuje (the Bengo flows out between Luanda and Ambriz).



All of these places are in the coastal plain but the sample described here came from the plateau not far from Malange. The range of *scalaris* extends through Central Africa and up into Kenya and Uganda.

The placing of *canescens* in the synonymy of *scalaris* will undoubtedly be questioned by some authorities. Mandahl-Barth (1957b) refers to *canescens* as an extreme form of *forskali* and mentions that the only material which he has seen came from a cattle trough on Lochinvar ranch, Northern Rhodesia. I have been fortunate in having material from this same locality breeding in the laboratory and have been able to study it in considerable detail. The male copulatory organ (Text-fig. 96) is characteristic for *scalaris*, having a wide proximal dilatation of the penis sheath and a very long epiphallus. Although the shells of the majority of the original Rhodesian specimens are completely smooth and lacking either ribs or carination many of the laboratory-bred specimens are clearly ribbed and some have a slight shoulder on the upper whorls. Morelet (1868) described *canescens* as having fine growth lines which appear as weak ribs on the upper whorls of some specimens. He reported that a number of individuals showed marked ribbing and carination of the upper whorls and he suggested that these might be hybrids between *canescens* and another species. Morelet also mentioned that Dunker's definition of *scalaris* was inadequate in that it failed to include some forms with shorter spires and others which are turriculate. A careful examination of the type series of *scalaris* (Pl. 9, figs. 1-3) shows a distinct carination on the apical whorls of two of the three specimens, also quite clearly marked ribs (Pl. 10). There is, therefore, no doubt that *canescens* is a form of *scalaris* and the definition of the species must include the presence of a slight carination and ribs on the upper whorls.

The form referred to under the name *B. scalaris* by Carvalho and Janz (1960) is undoubtedly *B. crystallinus* (Morelet).

***Bulinus crystallinus* (Morelet)**

Physa crystallina Morelet, 1868: p. 89, pl. 9, fig. 4.

Bulinus senegalensis; Janz & Carvalho, 1956.

Physa sp.; Casaca & Carvalho, 1955.

Bulinus scalaris; Carvalho & Janz, 1960.

MATERIAL. A total of seventeen shells was received from Dr. Morais de Carvalho, all collected in the neighbourhood of Salazar, Cuanza Norte in the Rio Moembege

FIGS. 83-95. *Bulinus forskali*. Figs. 83-90. Male copulatory organs and receptacula of specimens from Lagoa Dalagosa. (83-85); Lagoa Panguila. (86); Lagoa Quilunda. (87); Dondo. (88); Laboratory-bred Lagoa Panguila. (89 & 90). Fig. 91. Radula teeth of specimen from Dondo. Fig. 92. Aberrant central and first lateral, Dondo. Fig. 93. Aberrant first and fourth laterals, Lagoa Quilunda. Fig. 94. First, fifth and seventh laterals, Dalagosa. Fig. 95. Three aberrant centrals and two first laterals, Bom Jesus.

FIGS. 96-99. *Bulinus scalaris*. Fig. 96. Male copulatory organ of specimen from Lochinvar Ranch, Southern Rhodesia. Fig. 97. Receptaculum, Quionqua. Fig. 98. Mantle, Quionqua. Fig. 99. Radula teeth, Quionqua. Figs. 100 & 101. *Bulinus crystallinus*, receptaculum and male copulatory organ.

and its tributaries (Rio Camundai, Rio Conda, the irrigation system of a vegetable garden in Salazar and at Quifué on the Moembege above Salazar). September, 1954.

HABITAT. Casaca and Carvalho (1955) mention that in the area around Salazar they found freshwater snails only in the slow-flowing parts of the streams, particularly where the water was dirty and contained rotting banana leaves. Presumably these specimens were found under these conditions.

SHELL (Pl. II, figs. 4-7). The largest specimen in the sample measured 9.5 mm. long, 4.6 mm. wide, 5.8 mm. aperture length and 2.7 mm. aperture width. The mean length of the sample was 7.4 mm. The body whorl is about two-thirds of the total shell length and the spire is relatively short and pointed. The mean value of the ratio shell-length/aperture length at length 7.5 mm. is extremely low, only 1.67, and the value of the ratio length/aperture width at the same size is also low, 3.43. These two indices express the low spire and relatively great width of the shells, giving them the appearance of belonging to the *truncatus* rather than to the *forskali* species group. The whorls are markedly shouldered and regularly and strongly ribbed. The shells are of a reddish-brown colour.

ANATOMY. Examination of the shells showed that some still contained the dried bodies of the animals. Three of these specimens were carefully cracked and incubated for three days at 35° C. in a 0.5 per cent. solution of tri-basic sodium phosphate (van Cleave and Ross, 1947). This treatment did not restore the animals completely but it enabled some observations of the anatomy to be made. The mantle markings were large, irregular black blotches on a grey ground and the ridges on the underside showed that the material belonged definitely to the *forskali* group. All three of the specimens were fully mature and in one there appeared to have been a regression of the prostate suggesting that the functionally hermaphrodite stage of the sex cycle was passed and that the specimen was effectively female only. The male copulatory organs of two individuals were removed intact. The preputium in both was a little longer than the penis sheath, the proximal dilatation of the sheath was only a little narrower than the diameter of the preputium and the epiphallus was short (Text-fig. 101). The receptaculum seminis was seen intact in one specimen only and it was extremely large and sac-like with a relatively short duct (Text-fig. 100).

RADULA. The radulae of these specimens showed no obvious malformation and the teeth are similar to those of *B. forskali* from Dondo but with seven tricuspid laterals and seventeen to eighteen marginals.

The question of whether *B. crystallinus* is really a distinct species still remains unanswered for other members of the *forskali* group have not been found associated with it and it may be no more than a very extreme local form. It is the only member of the group so far recorded from the escarpment zone (the type locality is also in this zone, in the Golungo Alto district) of Angola and it appears to be confined to this region. Despite intensive searches of the Rio Moembege and its tributaries

over a period of three days in late October 1957 I was unable to find even empty shells of this species. Reference to Welwitsch's manuscript notes indicates that the original material was probably collected in February 1855 but collections in the same area were also made in October 1855 and October 1856.

The material described by Carvalho and Janz (1960) as *B. scalaris* is based on material from Salazar, the origin of the present specimens. They describe the shell characters in detail and show graphically how they can be distinguished from *B. forskali*. The copulatory organ which they describe and figure is not unlike that described here but they indicate that there is a long coiled epiphallus like that in *scalaris*. They do note that they also found material in Benguela and this may have been true *scalaris*.

Limnaea natalensis Krauss

Limnaeus natalensis Krauss, 1848: p. 85, pl. 5, fig. 15.

Limnaeus succinoides Morelet, 1866: p. 161.

Limnaea Bocageana Morelet, 1868: p. 86, pl. 7, fig. 3.

Limnaea Benguelensis Morelet, 1868: p. 86, pl. 6, fig. 4.

Limnaea sordulenta Morelet, 1868: p. 87, pl. 7, fig. 5.

Limnaea orophila Morelet, 1868: p. 87, pl. 7, fig. 4.

MATERIAL

Panguila (Lagoa), large lake on banks of Rio Bengo. 43 specimens. 8th November, 1957.

Quequesse (Lagoa), grass-choked swamp near Bazabom. 2 specimens. 13th November, 1957.

Tentativa (Fazenda), irrigation ditches on sugar-cane plantation and stream carrying effluent from factory. 103 specimens. 8th November, 1957.

Quissol (1), small stream two miles west of Quissol on Malange road. 9 specimens. 24th October, 1957.

Quissol (2), dam in Quastimbala stream. 10 specimens. 24th October, 1957.

Moembege (Rio), backwater of stream. 6 specimens. 30th October, 1957.

Cangombe, pools in stream bed. 48 specimens. 21st November, 1957.

Capemba and San José, in shallow seepage water and pools. 51 specimens. 21st November, 1957.

Cassinde Pequeno, in shallow pools in run-off from well. 24 specimens. 21st November, 1957.

Cassinga, backwater of Rio Cului. 3 specimens. 22nd November, 1957.

Cativa, washing place in River Cuango. 11 specimens. 23rd November, 1957.

Catoco, stream near village. 30 specimens. 21st November, 1957.

Cului (Rio), bridge on Vila Artur de Paiva-Dongo road. 14 specimens. 23rd November, 1957.

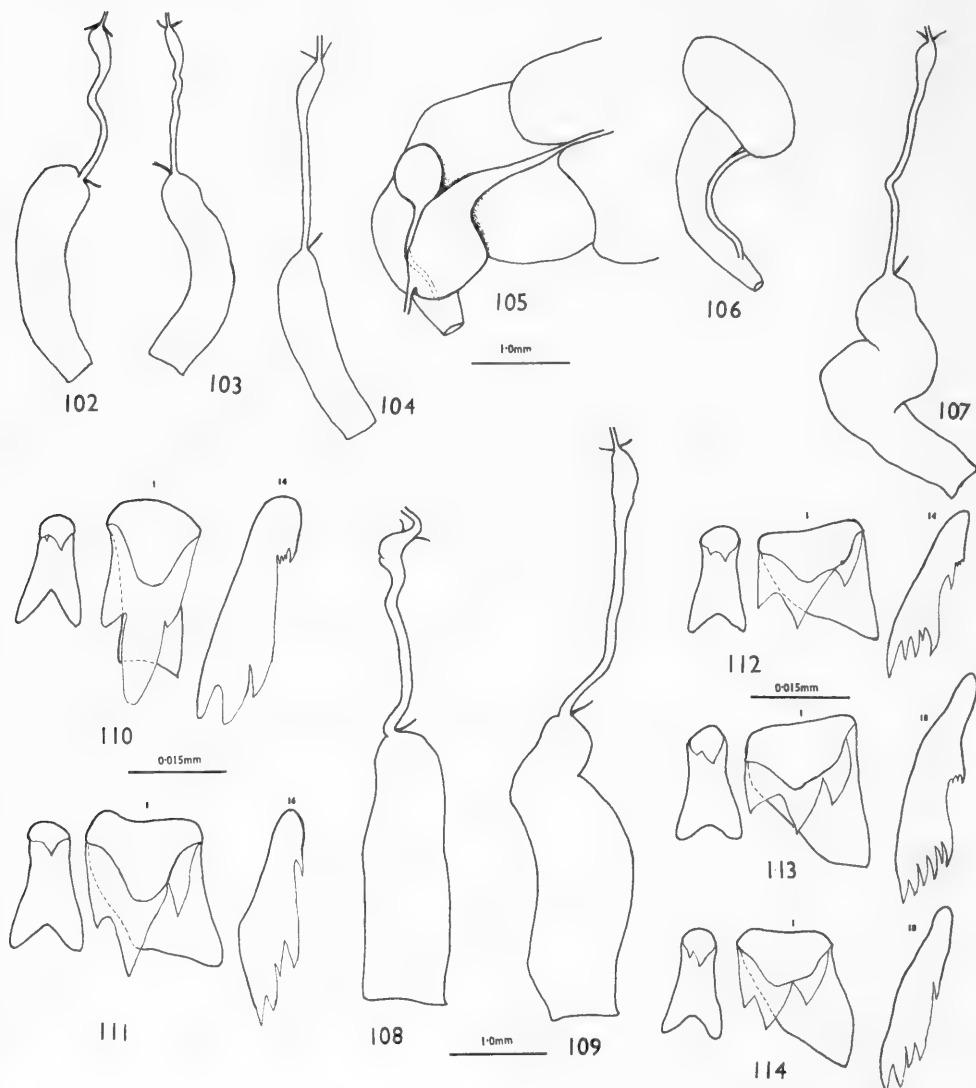
Gunda Vunjanganga, deep pool in stream bed. 4 specimens. 22nd November, 1957.

Quesso (1), intake of irrigation system for Granja Administrativa. 6 specimens. 21st November, 1957.

Quesso (2), marshy pools near bank of Rio Cubango. 1 specimen. 21st November, 1957.

Senga, stream through village. 2 specimens. 22nd November, 1957.

Vila Artur de Paiva, ditch carrying run-off from spring in town. 6 specimens.
21st November, 1957.



FIGS. 102-114. *Lymnaea natalensis*. Figs. 102-104. Male copulatory organs, Dongo. Fig. 105. Accessory genital glands showing swollen distal part of prostate, Dongo. Figs. 106 & 107. Receptaculum and male copulatory organ, Quissol (1). Figs. 108 & 109. Male copulatory organs, Fazenda Tentativa. Figs. 110-114. Radula teeth, Lagoa Panguila (110), Fazenda Tentativa (111), Quissol 1 (112), Capembe and San Jose (113) and Dongo (114).

HABITAT. *L. natalensis* is the most widely distributed species found in the present work. It was collected in a wide range of habitats from large lakes to small streams and pools, sometimes in very shallow water, usually on vegetation, either aquatic or emergent but also on mud. Some of the specimens from Lagoa Panguila were found just out of the water, crawling on sheltered parts of the emergent vegetation.

SHELL (Pl. 13, figs. 1-6). Although it is subject to considerable variation in detail the shell of *L. natalensis* is remarkably constant in its general characters. The shape is elongate-ovoid, succineiform and the spire is sharply pointed. The maximum width is just over half the shell length and the aperture length is normally three-quarters of the shell length. There is little microsculpture other than fine growth lines, clean shells have a shiny lustre but this is often obscured by algal growths. The shells are almost colourless, sometimes a very pale light brown; two of the samples collected in Angola (Capemba and Cassinde Pequeno) show well-marked zebrination with alternating light and dark bands. The columella is slightly twisted and the columellar margin is reflexed so that the umbilicus is closed. The outer lip of the aperture is the most variable character of the shell. It is always thin and sharp and it may curve outwards giving a smoothly ovoid aperture or it may be straight or even slightly incurved giving a rectangular appearance. The angle at which the outer lip meets the body whorl also varies from very acute to almost a right-angle. These characters appear to vary more between populations than within them, thus there is a tendency for the samples from the coastal plain to have the outer lip curved and meeting the body whorl at nearly a right-angle while the specimens from the Malange area also have the right-angled junction with the body-whorl but have the outer lip more flattened and those from the southern plateau region have the outer lip flattened and an acute upper angle.

The following table gives the dimensions in millimetres of some of the larger samples collected :—

Locality	Mean Length (Range in Brackets)	Mean Width	Mean Value l/ml (Range in Brackets)
Panguila	12.0 (4.6-19.2)	7.0	1.39 (1.26-1.62)
Tentativa	12.3 (5.9-18.4)	6.2	1.36 (1.09-1.50)
Cangombe	12.4 (8.6-18.9)	6.3	1.43 (1.20-1.71)
Capemba	10.5 (7.5-17.6)	5.75	1.34 (1.08-1.57)
Catoco	11.8 (7.2-16.5)	6.0	1.42 (1.31-1.57)

ANATOMY. The colour of the mantle varies considerably between populations. The most usual is a dark sepia ground colour with sparse white and black spots and usually a black bar near the pneumostome. Several of the samples from the southern plateau have the mantle almost uniformly black while others have a light grey ground colour with either black spots and blotches or a black reticulate pattern. Whatever the basic markings of the mantle in any population, it is nearly always lighter in colour in young specimens than adults. The male copulatory organ has the penis sheath and preputium roughly equal in length (Text-figs. 102-104, 107-109), the sheath always very slender with scarcely any proximal dilatation to

demarcate it from the vas deferens. There does not appear to be any constancy in the degree of coiling of the penis within the upper part of the sheath. All of the specimens examined had the distal end of the prostate swollen to some extent (Text-fig. 105). The duct of the receptaculum seminis is usually about the same length as the vagina and it is slender (Text-fig. 106); in some populations it is longer than in others and this is readily seen during dissection of mature snails for the sperm-filled receptaculum is bright orange in colour and in individuals with a long duct the sac can be seen lying well down on the left side of the body while in those with a shorter duct it is nearer to the mid-line.

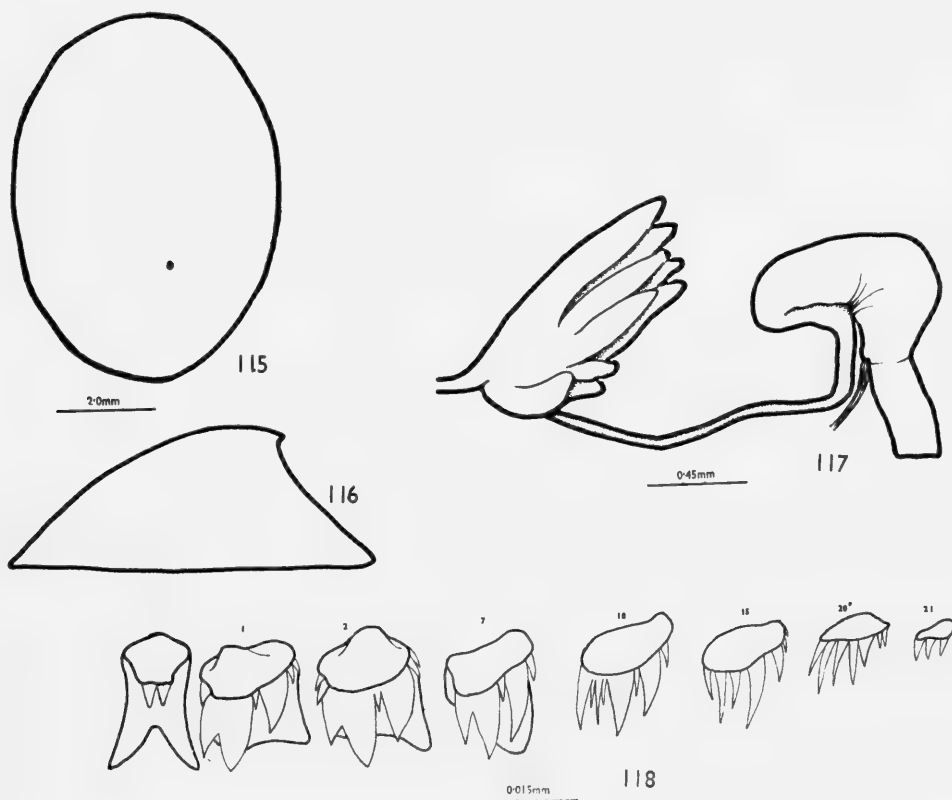
A number of the specimens dissected were heavily infected with larval trematodes and in several cases there is little doubt that the fluke concerned was *Fasciola gigantica*.

RADULA. The variation in form of the radula teeth in this species is comparable to that described by Berrie (1960) for *L. peregra* in Sweden. The central tooth is either asymmetrically bicuspid or almost symmetrical with a single cusp. There are usually 8–10 tricuspid laterals in which the endo- and mesocones are almost completely fused. The cusps on these teeth may be relatively short and broad in some populations (Quissol, Dongo, Capemba and San José, Text-figs. 112–114) or longer and more lanceolate (Tentativa, Text-fig. 111); those from Panguila (Text-fig. 110) have the tips of the cusps quite blunt and worn-looking even on the new teeth at the back of the radula. The marginals vary widely from a tri-cuspid form with serrations on the outer edge to more delicately comb-like forms with five to eight cusps all of roughly equal size.

L. natalensis was described by Krauss from Natal. Many subsequent authors have described and named other closely related forms from all over tropical Africa but Hubendick (1951) has suggested that there are no anatomical distinctions to support this division and refers them all to the synonymy of *L. natalensis*. Unpublished chromatographic studies in this laboratory have so far confirmed this opinion but Mandahl-Barth (1954) has retained a number of sub-species and states that *L. exserta* from Uganda differs from *natalensis* in that the distal part of its prostate is not dilated. The Lymnaeidae have provided a fruitful source of material for studies in infraspecific variation in several parts of the world and there is little doubt that the forms described from tropical Africa do not merit taxonomic distinction; Pilsbry and Bequaert (1927) go so far as to say "Few examples of nomenclature so futile and inane can be found, since the variations are far less marked than in any good series of *L. stagnalis* or *auricularia*". Morelet (1866) named *L. succinoides* (Pl. 12, fig. 4) but in 1868 he altered this to *L. benguelensis* to avoid confusion with *L. succinea* Deshayes, 1834 from India. This action is not justifiable from the nomenclatorial aspect since *succinoides* cannot be regarded as a homonym for *succinea* apart from which *L. succinea* Deshayes is a junior homonym for *succinea* Nilsson 1823. Both *succinoides* (= *benguelensis*) and *orophila* (Pl. 12, fig. 2) were described from the southern area of Benguela, the first from the coastal plain and the other from the Serra de Xella. It is difficult to see how Morelet was able to separate the two species on characters of the shells in the type series. No specimens

from either of the type localities of these species were collected during the present expedition but it is interesting to see that the acute upper angle of the aperture and straight peristome are characteristic features of both species as well as of my material from Huila Province. Similarly the original material of *sordulenta* (Pl. 7, fig. 3) from the coastal plain in the neighbourhood of the Rio Dande is reasonably well matched by the large samples recently collected in the same area. *L. bocageana* (Pl. 7, fig. 1) from the Malange area of the plateau is represented only by the two samples from Quissol neither of which have attained anything like the size of the type series (all of which are damaged).

The presence of larval stages of *Fasciola gigantica* in some individuals from all the areas studied indicates that this parasite is extremely widespread in Angola and is likely to be most difficult to control due to the varied ecological tastes of *L. natalensis*.



FIGS. 115-118. *Burnupia* sp. cf. *gordonensis*. Fig. 115. Outline of shell, dorsal. Fig. 116. Outline of shell, from left side. Fig. 117. Prostate and male copulatory organ. Fig. 118. Radula teeth.

***Burnupia* sp. cf. *gordonensis* (Melvill and Ponsonby)**

Ancylus (*Ferrissia*) *gordonensis* Melvill & Ponsonby, 1903: p. 606, pl. 31, fig. 2.

MATERIAL. About 100 specimens were collected in the Rio Moembege where it passes through the Agricultural Research Station near Salazar, Cuanza Norte. 29th October, 1957.

HABITAT. The stream is moderately fast-flowing between steep banks and heavily shaded by tall bamboo. There is very little emergent vegetation, the specimens were found in considerable numbers in two short stretches of the stream on bracts fallen from the overhanging bamboo and on similar débris. Other snails found were a single *Succinea concisa* on a partially submerged rock and three *Gyraulus costulatus* on tufts of emergent grass a short distance upstream of the *Burnupia* habitat.

SHELL (Pl. 8, figs. 17–19). The sample contained specimens ranging from 9.4 mm. long, 6.6 mm. wide and 3.8 mm. high (this was the largest undamaged specimen but two shells with broken margins were undoubtedly a little bigger) to almost newly-hatched individuals measuring 0.6 mm. long, 0.5 mm. wide and 0.1 mm. high. The majority of the specimens were in the 4.0–6.0 mm. shell length range. The mean dimensions of such a sample are not of any great use but the ratios of shell-width/length and height/length give fairly constant values in all but the youngest specimens. The mean values of these ratios for a sample of twenty specimens are width/length 0.72 ± 0.06 and height/length 0.32 ± 0.02 .

The apex of the shell is radially punctate, only slightly displaced to the right of the mid-line and not strongly curved backwards (Text-fig. 115). Both the anterior and left slopes are slightly convex while that on the right is almost straight and the posterior face is concave below the apex but more nearly straight lower down (Text-fig. 116). The sculpture consists of extremely fine wavy radial striae but this is only visible in the younger specimens. In the largest shells no sculpture at all is visible other than poorly defined, slightly irregular concentric growth lines. The colour of the shells is light brown and they are very thin and fragile.

ANATOMY. The gonad consists of a crescentic arrangement of follicles lying near the posterior part of the body beneath the digestive gland. The albumen gland is large, compact and whitish in colour, lying beneath the apex of the shell and above the stomach. The hermaphrodite duct is short with a few seminal vesicles protruding from it. The oviduct is long, thin-walled and very convoluted, it leads into a compact, thick-walled and glandular uterus which is also strongly convoluted. The vagina is short and opens beneath the gill about half-way back on the left side of the body. The receptaculum seminis is club-shaped and the duct is about equal in length to the dilated part. The sperm duct is short and thin-walled, the prostate consists of a fan-shaped arrangement of six or seven long diverticula and three or four short ones opening into an atrium from which the vas deferens runs a short distance in the body wall (Text-fig. 117). Within the head cavity the vas deferens is short and thickened, the male copulatory organ is

large and the penis sheath is usually partly evaginated into the preputium which is a little narrower and shorter than the sheath.

Seven out of ten specimens which were dissected were found to be infested with a larval trematode the cercaria of which was furcocercous and, although their state of preservation was poor, they showed some resemblance to *Cercaria oudtshoornia*, described by Porter (1938) from *Burnupia capensis* in Cape Province, South Africa.

RADULA. The radulae of six specimens were examined and proved to be fairly uniform. The median teeth are relatively long, slender and bicuspid. There are seven or eight laterals, basically tricuspid with the endocone and mesocone only partially separated and with very small accessory cusps on the inner margin of the endocone and the outer edge of the ectocone. Most of the laterals have a very small interstitial cusp between the meso- and ectocones. The marginals are about fourteen in number and the outermost ones are simple and comb-like (Text-fig. 118). One of the radulae showed the endo- and mesocones of the first lateral to be fused completely on one side only.

The affinities of this material are not easy to determine and it is with some misgivings that it is referred to *B. gordonensis*. The taxonomy of the African Ancyliidae is in a very confused condition as is to be expected in a group with so few clearcut characters. It was hoped that the ratios of shell dimensions might be of some use and the ratios of the twenty-three species of *Burnupia* listed by Walker (1923), Pilsbry and Bequaert (1927) and Mandahl-Barth (1954) were worked out. Of these, sixteen fell within the standard deviation of the width/length ratio of the present sample and only one within the range of the height/length ratio, all of the others (except *B. kempi* (Preston)) being relatively higher. The one species having a similar height/length proportion, *B. capensis* Walker, has a considerably smaller width/length ratio. Comparison with the types or paratypes of a number of species in the collection of the British Museum (Natural History) showed that the majority of the specimens in the sample were more like *B. gordonensis* (Pl. 8, figs. 20–22) than any of the others. The characters of the radula are also more like those described by Walker for *gordonensis* than for any other and include the small accessory cusps on the inner margin of the endocones as well as the interstitial cusp between the meso- and ectocones of the lateral teeth, characters which led Walker to suggest that the radula from which his observations were made was abnormal. Examination of three radulae labelled as *B. capensis gordonensis* in the Gwatkin collection shows them to be apparently similar to the present material but unfortunately the Gwatkin radulae of *Burnupia* are all unstained and therefore not easy to interpret. In the Piele collection there is a radula of a paratype of *B. obliqua* (Krauss) and this is very similar to the present material, but a specimen labelled *B. capensis* has much shorter and more triangular cusps. Walker mentions that some of the samples of *gordonensis* which he examined contained several specimens in which the shell was strongly laterally compressed and one such individual was found in the Angolan sample, in fact it bore a striking similarity to *B. stenochorias* (Melvill and Ponsonby) but the radula is the same as that of the

other specimens in the sample and quite unlike that of *stenochorias*. It is perhaps worth mentioning in passing that there is a radula of a paratype of *stenochorias* in the Piele collection and that it differs from the description and figure given by Walker for this species in that the endo- and mesocones of the laterals are not completely fused and, in fact, the endocone is subdivided into two small cusps.

This species appears to be the first ancyclid recorded from Angola (Walker restricted the distribution of *gordonensis* to streams flowing into the ocean between Durban, Natal and Grahamstown, Cape Province) and it is interesting that it was the only one found during the present investigation.

Succinea patentissima Pfeiffer

Succinea patentissima Mencke, Pfeiffer, 1853: p. 52.

Succinea (Oxyloma) patentissima; Quick, 1936.

MATERIAL

Lalama (Lagoa), large lake near Rio Bengo. 1 specimen. 14th November, 1957.

Lumango (Lagoa), small lake near Rio Bengo. 12 specimens. 14th November, 1957.

Quequesse (Lagoa), grass-choked swamp near Bazabom. 1 specimen. 13th November, 1957.

HABITAT. The three localities in which this species was collected were all on the edge of lakes with a dense fringe of grasses and reeds. The snails were found both in the water and on the stems of plants above the surface.

SHELL (Pl. 14, fig. 6). The shell is little more than a flattened cap which fits over the visceral mass and is not large enough to accommodate the head and foot of the animal. There is a diminutive spire at the apex and this is sharply pointed. The outline of the shell is roughly oblong and the aperture is wide. The columella has a pronounced fold near its upper end but in some individuals this is less well-marked. The shells are thin and translucent and of a pale yellowish-brown colour. The largest specimen examined was 12.6 mm. long and 6.5 mm. wide and the smallest 9.6 mm. long and 5.1 mm. wide.

ANATOMY. The anatomy of this species has been described in detail by Quick (1936). The common genital opening is well forward on the right side of the body and is a simple slit. The general anatomy of the reproductive system and details of the male copulatory organ are shown in Text-figs. 119, 120. The gonad lies near the apex, embedded in the digestive gland and from it arises the hermaphrodite duct, relatively thick and light brown in colour at its proximal end but colourless distally. Just before the hermaphrodite duct enters the albumen gland it gives off two short, blunt unpigmented diverticula which Quick (loc. cit.) describes as seminal vesicles but which Duncan (1961), describing the anatomy of *S. pfeifferi*, suggests are fertilisation sacs. The albumen gland is larger than the gonad and is closely applied to the upper wide loops of the oviduct, embedded in which lies

the prostate. The lower part of the oviduct is narrower and sharply coiled and joins imperceptibly into the straight, slightly dilated vagina. The slender receptaculum seminis duct arises from the vagina and runs straight back to the large spherical receptaculum which lies at about the level of the distal part of the albumen gland. The vas deferens runs forward from the prostate almost to the genital atrium and then turns back and lies closely applied to the penis sheath which it enters subterminally at the proximal end. The penis retractor muscle is a prominent feature attached to the extreme end of the sheath. Within the sheath there is a long coiled epiphallus and the penis has a small lateral diverticulum.

RADULA. Each row of teeth is arranged in a shallow M-shape. The tricuspid centrals have a large, dagger-like mesocone with a smaller cusp on either side. The inner laterals are basically bicuspid, apparently consisting of a large mesocone and smaller ectocone and the marginals have five or six cusps including an endocone and subdivided ectocone. Quick noted that the transition from laterals to marginals is not clear in this species since there may be irregular subdivision of the ectocone in the laterals. In this material there are usually five or six bicuspid laterals then about four transitional teeth in which the ectocone is divided and fifty to sixty marginals (Text-fig. 121).

Succinea patentissima appears to be a manuscript name of Mencke and the first published description is that of Pfeiffer. The type locality is given as Port Natal and Connolly (1939) records it also from Zululand, Transvaal, Southern Rhodesia and Lourenzo Marques.

The inclusion of *Succinea* in a work on freshwater gastropods is questionable from the systematic point of view but fully justified ecologically because of the frequency with which these snails are found when searching for purely aquatic forms.

Dr. Quick has been kind enough to examine my material of this and the following species and it is to him that I am indebted for the identifications. The material from Lumango and Quequesse he considers to be typical of the species but the single specimen from Lalama has the columellar fold less well-marked and the distal part of the oviduct is longer.

The only species of *Succinea* previously recorded from Angola is *S. badia* Morelet (Pl. 14, figs. 1-3) collected by Welwitsch from the Islands of Calemba in the Cuanza river to the south-south east of Malange on the plateau.

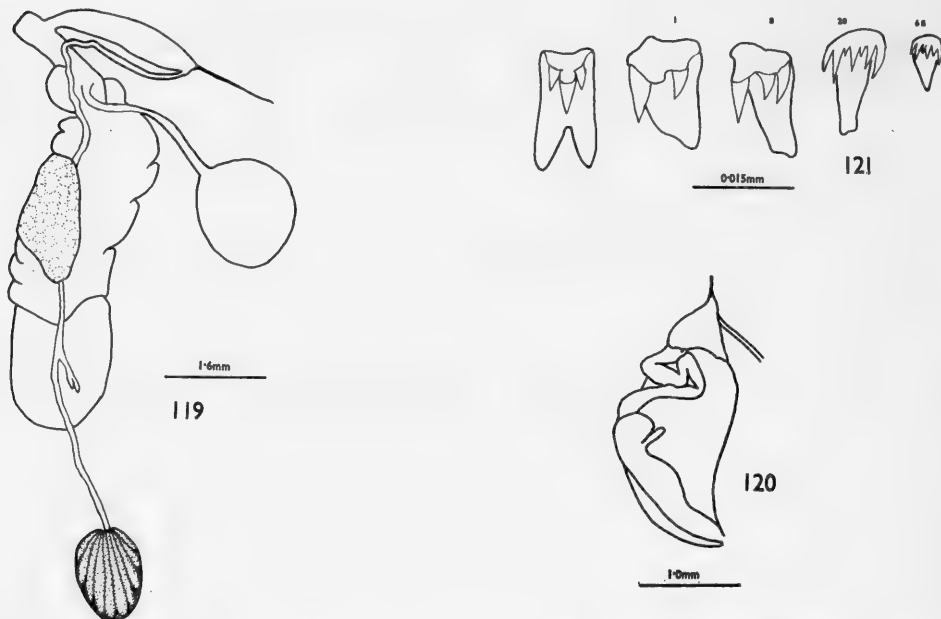
Succinea concisa Morelet

Succinea concisa Morelet, 1848: p. 351.

MATERIAL. *Moembege* (1) (*Rio*), river passing through Agricultural Research Station, Salazar, Cuanza Norte. 1 specimen. 29th October, 1961.

HABITAT. The stream was moderately fast-flowing between steep banks and heavily shaded. The specimen was found on a moss-covered stone sticking out of the water in mid-stream.

SHELL. The specimen was damaged and not well preserved. The shell is better developed than in the preceding species with a more marked but less sharply pointed spire. It is heavily encrusted with mud and detritus, a feature noted by Quick (1936) to be characteristic for the species.



FIGS. 119-121. *Succinea patentissima*. Fig. 119. Whole genital system, ventral view. Fig. 120. Male copulatory organ, penis-sheath opened to show penis. Fig. 121. Radula teeth.

ANATOMY. The state of preservation of the specimen was not sufficiently good to permit a detailed examination of the anatomy but one or two features were observed which differ greatly from *S. patentissima* and which are also described by Quick. There is a dilatation of the hermaphrodite duct which is not seen in *patentissima*. The albumen gland is longer and narrower in *concosa*, the prostate and receptaculum seminis are relatively smaller, the oviduct is less tightly coiled, the vas deferens runs straight to the proximal end of the penis instead of looping forward and the male copulatory organ is small. According to Quick there is no penis sheath in this species but it is not possible to confirm this from the single specimen available. The radula of this specimen was unfortunately lost.

S. concisa (Pl. 14, figs. 4, 5) was originally described from material collected on the banks of the Gaboon river, and Quick's specimens on which his anatomical studies were based came from Sierra Leone, but he also mentions shells from Zanzibar. Pilsbry (1919) quotes Boettger as recording the species from the Congo at Banana Creek.

Lanistes ovum Troschel

Lanistes ovum Peters, Troschel, 1845: p. 215.

Ampullaria ovum; Morelet, 1868.

MATERIAL

Tentativa (Fazenda), stream carrying effluent from sugar factory. 7 adult specimens. 8th November, 1957.

Matoz (Lagoa), drainage ditch beside small lake on the edge of Fazenda Tentativa. 19 adult, 3 juvenile specimens. 8th November, 1957.

Panguila (Lagoa), large lake near mouth of Rio Bengo. 4 adult and 5 juvenile specimens. 8th November, 1957.

Quilunda (Lagoa), large lake on the banks of Rio Bengo. 6 adult specimens. 14th November, 1957.

Dalagosa (Lagoa), lake on flood plain of Rio Cuanza. 1 adult and 5 juvenile specimens. 13th November, 1961.

HABITAT. This species appears to thrive in still water and seems to be tolerant of fairly polluted conditions. The numbers collected at the localities mentioned above are not an index of their relative abundance since their bulk prevented the accumulation of very large samples.

SHELL (Pl. 15, fig. 4). The spire is well developed and the whorls are gently rounded. The colour varies from dark horn to glossy brown but many specimens from muddy habitats have the shells heavily coated and the colour is completely obscured. The aperture is shaped like an inverted comma, the outer margin is regularly curved and meets the body-whorl at a slightly acute angle and the columella is also gently curved. The columellar margin is very slightly reflexed but all of the specimens have the umbilicus quite open. The only sculpture is of fine growth lines but a few of the smaller adult shells show a very weak malleation of the body whorl. The largest specimen collected has four and a half whorls and is 36 mm. high, 27.5 mm. maximum diameter and 19 mm. aperture height. Mean dimensions of the adult shells from Lagoa Matoz are 23.7 mm. high, 20 mm. maximum diameter and 14 mm. aperture height. Very young juvenile shells are wider than high at the 1-2 whorl stage, colourless and completely transparent.

RADULA. The massive central tooth has a large, pointed median cusp with three smaller cusps on either side. The lateral has a very well developed mesocone, with two smaller outer cusps and a similar-sized endocone and the two marginals are bicuspid with one cusp much larger than the other (Text-fig. 122).

Morelet recorded this species in Welwitsch's collection from Bembo lake on the Dande river, also at Funda, Foto and Moembege. One of the Welwitsch specimens in the British Museum (Natural History) collection (Pl. 15, fig. 1) compares well with my material but is much larger. At five and a half whorls it is 46 mm. high, 40 mm. maximum diameter and 25 mm. aperture height. These dimensions are close to those of another specimen in the collection reputed to be a paratype of *L. ovum* (Pl. 15, fig. 2) originating from the Cumming collection.

My material appears to be very similar to that illustrated by Pilsbry and Bequaert (1927) as *L. adansoni* Kobelt and the measurements agree well. Boettger (1913) considers *adansoni* to be a sub-species of *ovum* but reference to Kobelt's (1911) description suggests that his species (from the Senegambia region) is distinct from *ovum* since its maximum diameter is greater than its height and it is much more widely umbilicate. Kobelt's illustration of *adansoni* looks more like the reputed type specimen (in the British Museum collection) of Morelet's (1860) *L. holostoma*, from Guinea.

L. ovum appears to have great resistance to desiccation. Morelet records that Welwitsch collected blocks of dried mud from the banks of one of the lakes in the coastal plain and these were put in a store room in Luanda and forgotten for two years. When they were eventually placed in water a number of live *Lanistes ovum* emerged.

Lanistes libycus (Morelet)

Ampullaria Libyca Morelet, 1848: p. 28, pl. 3, fig. 9.

MATERIAL. A single live specimen found in the papyrus swamp fringing the Rio Lucalla above the Duque de Braganza falls. 25th October, 1957.

HABITAT. At the time the specimen was collected the river was low and the living individual was found in a small pool on a mud bank in the papyrus swamp. A number of broken dead shells were seen, suggesting that the snails had been killed by some predator. During the later part of the wet season the river here probably runs very swiftly.

SHELL (Pl. 15, fig. 3). The general shape is globose, sinistral and low-spined, the apex is missing. There are about four whorls and the shell is 27 mm. high, 25.5 mm. wide and the aperture is 19 mm. long. The aperture is roughly oval, slightly narrower above, the outer lip regularly curved and the columella straight. The columellar margin is reflexed, partially closing the umbilicus. The operculum is thin and horny with very fine concentric lines and the nucleus is eccentric, near to the columella. The colour of the shell is drab yellowish-brown with dark brown longitudinal bands which are broader near to the base of the whorl. The internal colour is bluish-white and the bands are purplish-brown colour. The upper part of the whorls is flattened but there is no sharp shoulder angle. There is no carination around the umbilicus. This specimen was a mature female.

RADULA. The radula teeth are very similar to those of *L. ovum* and the only features which appear to be different in *L. libycus* are the reduced outer cusps of the central tooth and the sharply pointed endocones of the laterals (Text-fig. 123). These characters are very variable and if more than one radula of *libycus* were available the range of variation in the two species would probably be found to overlap.

Lanistes libycus (Pl. 16, figs. 5, 6) was described from lakes in Gaboon and has a fairly wide distribution in West Africa. It has not been previously reported from Angola but there is a sample of four shells in the collection of the British Museum (Natural History) from an unspecified locality in the territory. These shells differ

from the present specimen in that none has the columellar margin reflexed and all have a trace of an umbilical carination. In their characters the sample shows a range of variation which covers the characters of the single specimen from Duque de Braganza. The type series consists of three adults and one juvenile specimen, all have a relatively well-marked shoulder carination but the angle around the umbilicus is poorly developed in the larger individuals. The type series are all lighter in colour than my Angolan specimen and the band pattern is not so well marked.

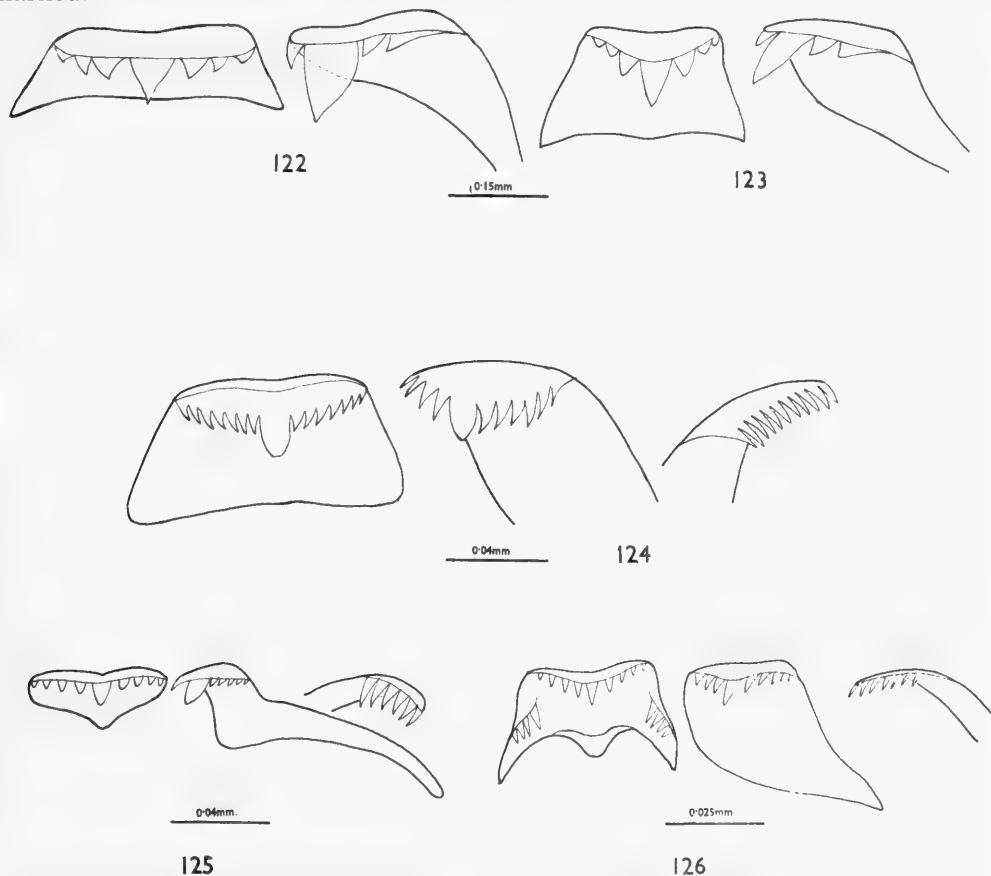


Fig. 122. *Lanistes ovum* radula teeth. Fig. 123. *Lanistes libycus* radula teeth. Fig. 124. *Bellamya unicolor* radula teeth. Fig. 125. *Melanoides tuberculata* radula teeth. Fig. 126. *Gabbia kisalensis* radula teeth.

***Bellamya unicolor* (Olivier)**

Cyclostoma unicolor Olivier, 1804: p. 39, pl. 31, figs. 9a, 9b.

Viviparus (Bellamya) monardi Haas, 1934.

MATERIAL. *Cuije* (Rio), moderate sized, muddy river, collection made near bridge on Malange-Cangandala road. 6 specimens. 24th October, 1957.

HABITAT. On sticks and debris and on the mud banks of the river which was flowing quite swiftly.

SHELL (Pl. 14, figs. 7, 8). The adult specimens are all very similar in size, one slightly larger than the rest measures 17.5 mm. high, 14.0 mm. wide, 8.5 mm. aperture height and 7.5 mm. aperture width. The colour is drab olive-green and the shell is shiny. The apical whorls have a slight upper carination forming a fairly well defined shoulder and there is also a well-marked peripheral angle which weakens in the largest specimen. The outline of the whorls between the two angles is nearly straight. All of the specimens have the umbilicus open and there is a well-marked umbilical canal. The aperture is nearly circular in older specimens, the columella is gently curved and its margin is not reflexed. The operculum is very thin, corneous and slightly concave. The micro-sculpture consists of fine well-developed spiral lines near the upper part of the whorls and around the umbilicus but the sides of the whorls are smooth. The young, of which eight were found in a single uterus, have the shell quite transparent and the angles most clearly marked and accentuated by the presence of filamentous projections of the periostracum. The spiral sculpture is strongly developed and they are born at about the three whorl stage.

RADULA. The large central tooth has a strong median cusp and seven sharply pointed smaller cusps on either side of it. The lateral and inner marginal teeth are similar to one another with a well-developed middle cusp and five or six curved, sharply pointed smaller ones on either side and the outer marginals are uniformly pectinate (Text-fig. 124).

Bellamya unicolor has a wide distribution in the African continent. Originally described from Egypt, it has been reported by Pilsbry and Bequaert (1927) from several localities in the Congo drainage and the present record appears to be on the extreme edge on the range of the genus (*Bellamya* = *Viviparus*) shown by Pilsbry and Bequaert. However, Haas (1934) described *Viviparus* (*B*) *monardi* from two places in the Cunene system in South Angola, and Connolly (1930), records *B. leopoldvillensis* (Putzeys 1898) from South-west Africa near the Angolan border and remarks that several of the west African species (including *unicolor*) are very similar and may be identical. Mandahl-Barth (1954) has reduced the large number of species described from Lake Victoria to two, *B. unicolor* and *B. jucunda* but he has retained most of the other names as sub-species. No useful purpose would be served by attempting to relate the present small and rather isolated sample with any of these sub-species. Haas' specimens of *B. monardi* from southern Angola are about twice the size of the largest individual in my sample but apart from this there seems to be no justification for regarding them as separate species.

***Melanoides tuberculata* (O. F. Müller)**

Nerita tuberculata O. F. Müller, 1774: p. 191.

Melania recticosta E. von Martens, 1882: p. 248.

MATERIAL

Tentativa (Fazenda), irrigation ditches of the sugar plantation. About 80 specimens. 8th November, 1957.

Quilunda (Lagoa), very common on stones and amongst debris on the beach of this large lake near the Rio Bengo. About 50 specimens. 14th November, 1957.

Queso (1), intake of the irrigation system for the Granja Administrativa, a single shell collected by Dr. Guedes de Carvalho in October, 1957.

HABITAT. The three localities are all quite different, the irrigation ditches on Fazenda Tentativa had sluggish, muddy water, the intake of the irrigation system at Queso is fast-flowing and clear and Lagoa Quilunda is a large, open lake with clear water and, at the point where the specimens were collected, the bottom is stony and there is a beach of what appears to be limestone shingle.

SHELL (Pl. 16, figs. 1, 2). The shells of all three lots are superficially different. Those from Fazenda Tentativa have a buff ground-colour with spirally arranged rows of red-brown spots on the lower whorls. These spots are so regularly placed that they also form well-defined transverse rows. The sculpture of the upper whorls consists of two to four spiral ribs but these disappear below the fourth or fifth whorl and the lower part of the shell is almost smooth. The aperture is oval, acutely angled above, the columella is gently curved and light in colour and the columellar margin is reflexed, completely closing the umbilicus. The largest specimen in the sample is 19 mm. high, 8 mm. wide and has an aperture height of 6.5 mm. The sample does not contain many young specimens and the mean shell length is about 14 mm. The specimens from Quilunda are rather smaller and there is a greater number of juveniles in the sample. The shells are extremely light in colour and the suture is shallow. The spots on the lower whorls are either absent or very poorly developed but there is a well-marked dark brown band below the suture and the base of the body whorl has several spiral ribs the presence of which is sometimes accentuated by narrow, light brown bands running between them. The single specimen from Queso has the apex of the shell missing (this feature is less common in the other two samples than is usual in this species), the ground colour is buff with a pink tinge and the spirally arranged red-brown spots are very well marked on all the whorls. There are well developed spiral ribs on all of the whorls, giving the shell a rougher appearance than any of those in the other samples.

The species is viviparous and possibly parthenogenetic. All of the specimens which were dissected had embryos in the uterus, usually up to ten in a graded series of sizes from five to six whorls downwards but one specimen from Tentativa had over a hundred very small embryos, some without shells. The embryonic shells have the spiral ribs well marked and they also have irregular, coarse transverse ribs. No differences could be found between the embryonic shells of specimens from Quilunda and Tentativa.

RADULA. Radulae from both of the large samples were examined and no differences between them were found. The central tooth is small and roughly triangular with a well developed median cusp and four smaller ones on either side. The laterals

have a long tail-like base and seven cusps, the second from the inside edge being considerably larger than the others. The marginals are pectinate with six to eight cusps of equal size (Text-fig. 125).

Melanoides tuberculata is a widespread species whose distribution in Africa has been the source of some controversy. It was originally described from India and Pilsbry and Bequaert (1927) show its range extending from the west coast of North Africa through the Middle East, India, and the Malay Peninsula to southern China and Borneo. In Africa, however, they show it extending as far south as the Transvaal on the eastern side but they claim that it is absent in tropical West Africa and the Congo drainage where it is replaced by a large complex of related species. Connolly (1930) records *M. tuberculata* and *M. victorae* (Dohrn) from South-west Africa, thus extending the range of *tuberculata* well beyond the south-west limits set by Pilsbry and Bequaert. In 1939 Connolly commented that he only retained the name *victorae* to distinguish the smoother forms from the more usual tuberculate type and he was obviously not convinced that *victorae* was a distinct species. Mandahl-Barth (1954) found it necessary to distinguish between three sub-species of *tuberculata* in Uganda, one of which he described as new. There seems to be little justification for the separation of different forms of such a variable species, particularly when, if the animal is parthenogenetic, the characters of the founder member of a population may be of the greatest importance in determining the nature of that population.

The only previous Angolan record probably relating to *M. tuberculata* is von Martens' (1882) species *Melania recticosta* described from the Murie stream, a tributary of the Rio Cuanza on its north bank. It is interesting that Welwitsch did not collect *M. tuberculata* from Lagoa Quilunda because in November 1957 it was undoubtedly the dominant gastropod species in the lake. Fishermen on the lake-shore showed me the stomachs of several freshly-caught catfish which were distended with large numbers of these snails.

***Gabbia kisalensis* (Pilsbry and Bequaert)**

Bulimus (*Gabbia*) *kisalensis* Pilsbry & Bequaert, 1927: p. 216, fig. 17.

MATERIAL. *Cuije* (Rio), moderate river, collection made near bridge on Malange-Cangandala road. 16 specimens. 24th October, 1957.

HABITAT. On sticks and debris in the river, collected together with *Bellamya unicolor* and, at the time of collecting, thought to be the young of that species.

SHELL (Pl. 14, fig. 9). Small, globose, pale horn colour, spire short, often missing, aperture almost circular, columella gently curved and outer lip thickened. The shells are perforate but the umbilical slit is narrow. The largest whole specimen collected has three and a half whorls and is 4.6 mm. high, 4.3 mm. wide and the aperture is 2.7 mm. long by 2.2 mm. wide. The mean shell-length of the whole sample is just over 4 mm. and in the smaller specimens (about 3.5 mm. high) the height and width are the same. The operculum fits exactly into the aperture, it is calcareous and has a small spiral nucleus near the centre surrounded by a wide band of concentric growth lines.

ANATOMY. Half of the specimens were dissected and only two males were found. The copulatory organ has a lateral lobe a little longer than the penis but of roughly uniform width. The vas deferens coiled within the head cavity is extremely long.

RADULA. The central tooth has a sharp, narrow median cusp with four smaller ones on either side and four cusps pointing inward and downward on the sides of the basal plate. The laterals are simple with an off-centre major cusp and about eight others and the marginals have seven equal-sized cusps (Text-fig. 126).

The genus *Gabbia* appears to be mostly confined to eastern Central Africa, particularly in the great lakes region, and the area around Lake Chad. The present record extends the general range by a considerable distance in a south-westerly direction. My material seems to be sufficiently close to *kisalensis* to justify its inclusion in that species despite the greater size of the Angolan form and its greater height/width ratio. From the small specimens in my sample it seems that this ratio definitely increases with growth of the animal and it is probable that in shells as small as those recorded by Pilsbry and Bequaert the relationship between these two dimensions is reversed.

ZOOGEOGRAPHY

The latitudinal range of Angola extends southward from the warm, humid regions of the Congo toward the arid area of the Kalahari desert. Longitudinally the territory can be divided into three topographical regions, in the west a coastal plain of varying width, inland from this a forested escarpment zone, steep and narrow in the south, wider and more gently sloped to the north and an inland plateau extending for many miles to the east, ranging in height between about 3,000 and 5,000 feet. The plateau is divided into northern and southern parts by the Bailundo highlands, an elevated ridge running from south-west to north-east which forms an effective watershed between the major river systems of the Cuanza and Cunene and tends to divide the head-waters of the Zambesi drainage from those of the Congo.

Hall (1960) has given an excellent general description of the topography of the country with particular reference to the importance of the escarpment zone in the distribution of the bird fauna and in another paper the same author (1960a) provides a useful synopsis of the vegetational regions. I have used these two papers together with an unpublished essay on the flora of southern tropical Africa kindly lent to me by Mr. A. W. Exell to supplement my own observations on the areas in which my collections were made. There were four of these areas, the first in the coastal plain around Luanda from the Rio Lifune in the north to the Rio Cuanza in the south, the second in the escarpment zone around Salazar, the third on the plateau around Malange from Duque de Braganza in the north to Pungo Andongo in the south-west and the Rio Cuije in the south-east and the fourth on the southern part of the plateau in the Ganguelas region centred on Vila Artur de Paiva and extending south from Cativa to Cassinga between the Cubangue and Cubango rivers. The accompanying table summarises my own collections on a regional basis and additional information from the literature is included in the account of each area.

	Coastal Plain	Escarpment Zone	Northern Plateau	Southern Plateau
PLANORBIDAE				
<i>Biomphalaria salinarum</i>				x
<i>Biomphalaria pfeifferi</i>				x
<i>Biomphalaria</i> sp.			x	
<i>Anisus misellus</i>	x		x	
<i>Gyraulus costulatus</i>		x		x
<i>Lentorbis benguelensis</i>	x			
<i>Segmentorbis kanisaensis</i>	x			
<i>Bulinus globosus</i>	x	x		
<i>Bulinus africanus</i>				x
<i>Bulinus angolensis</i>			x	x
<i>Bulinus truncatus rohlfsi</i>	x			
<i>Bulinus forskali</i>	x		x	
<i>Bulinus scalaris</i>			x	
<i>Bulinus crystallinus</i>		x		
<i>Lymnaea natalensis</i>	x	x	x	x
<i>Burnupia gordonensis</i>		x		
<i>Succinea patentissima</i>	x			
<i>Succinea concisa</i>		x		
<i>Bellamya unicolor</i>			x	
<i>Lanistes ovum</i>	x			
<i>Lanistes libycus</i>			x	
<i>Gabbia kisalensis</i>			x	
<i>Melanoides tuberculata</i>	x			x
LYMNAEIDAE				
ANCYLIDAE				
SUCCINAEIDAE				
VIVIPARIDAE				
PILIDAE				
BITHYNIIDAE				
THIARIDAE				

The Coastal Plain

The area is rather flat and featureless apart from the large rivers flowing from east to west which dissect it. The climate of Luanda is defined by Queiroz (1953) as arid tropical and the vegetation in the area visited is mostly of an open grassland type with baobabs near water and a sprinkling of euphorbias elsewhere. Further inland and to the north and south of Luanda there are areas of mixed woodlands and savannah grasslands with acacias, while a strip running south from Benguela is defined as semi-desert and this grades into desert on its south and west sides.

Because of the flat terrain the rivers in this area are slow-moving in the dry season and flood extensively in the rains. There are large depressions on the flood plains of the rivers, some several miles across, which become filled annually and many of them persist throughout the year as large, shallow, muddy lakes, typical examples of which are Lagoa Panguila on the Bengo and Lagoas Dalagosa and Guimbe on the Cuanza. Such lakes usually have a dense cover of waterlily and lotus and provide excellent habitats for mollusc species favouring still water with full sun exposure. It seems probable that the irrigation systems of the Fazenda Tentativa on the Dande and the Fazenda Libongo on the Lifune may have replaced this type of shallow, muddy lake. A second kind of lake is that which does not necessarily have any regular river connection and is deeper than the preceding type, usually without heavy lily-cover but with a thick fringing swamp of papyrus or reeds. Examples of this kind are Lagoas Lalama and Lumango near the Bengo and in these the snail fauna is usually less dense than in the first type but normally includes *Succinea* and a greater variety of small planorbids. A third type of lake is large, open and relatively deep, more or less without lily-cover and with little marginal vegetation. Here there is some wave action and the snails are mostly confined to sheltered places or are found a foot or two below the surface, they may be abundant but the number of species is fewer. Only two lakes of this sort were seen, Cabemba on the Cuanza and Quilunda near the Bengo. During the rainy season there are undoubtedly many smaller temporary water bodies but these were only just appearing towards the end of my work in the area and none were examined.

The dominant pulmonate species found in the Coastal Plain are *Bulinus globosus*, *B. forskali* and *Lymnaea natalensis*. *Anisus misellus* is common and *Segmentorbis kanisaensis* and *Lentorbis benguelensis* are probably widely distributed. *Bulinus truncatus rohlfsi* was found only in Lagoas Panguila and Cabemba, on both occasions on a species of *Ceratophyllum* which was particularly abundant in both of these lakes. *Succinea patentissima* probably occurs wherever the presence of fringing swamps or emergent grass provides a suitable habitat. Although *Bulinus scalaris* was not found in the coastal plain during the present visit it must be common in temporary water bodies during the rains from the frequency with which it was collected by the early explorers. The commonest prosobranch is *Lanistes ovum*, particularly in slow-moving, dirty water and *Melanoides tuberculata* was abundant in the two localities where it was found. The collection in the British Museum (Natural History) contains a sample of *Pila occidentalis* (Mousson) and a series of *Cleopatra bulimoides* (Olivier) both from the Mossamedes area in the south of the

coastal plain, also a few shells of *Pachymelania fusca* (Gmelin) from the Rio Tapado near Benguela but none of these species was found around Luanda.

The Escarpment Zone

The description of the escarpment zone given by Hall (1960b) applies mainly to the steep region in the south while the only part which I visited was the area around Salazar where the rise is more gradual. Salazar is at an altitude of about 2,500 feet, to the east the land rises steadily toward Malange but to the west it slopes away more steeply. Queiroz (1953) describes the climate as humid temperate; although this may be technically correct the term temperate is inclined to have a rather different connotation as a general geographical classification and the vegetation in the area is of a degenerate rain-forest type.

Because of the topography most of the streams are fast-flowing and throughout much of their length they are heavily shaded, two physical characteristics which discourage many tropical freshwater snail species. In the immediate area of Salazar however there is some open country and for a short distance the gradient of the Rio Moembege is less steep. In this part of the stream both *Bulinus globosus* and *Lymnaea natalensis* were found and in the same area Dr. Morais de Carvalho collected the specimens of *Bulinus crystallinus* described in this paper. It is significant that the only other definite record for this species (the original material collected by Welwitsch) is also from the escarpment region, a little to the north in the Golungo Alto district. Downstream from Salazar the Moembege becomes more fast-flowing and heavily shaded and it was in a very short stretch of the river under these conditions that *Burnupia* sp. cf. *gordonensis* was common and two specimens of *Gyraulus costulatus* and one of *Succinea concisa* were found. The river and one of its tributaries were carefully searched for about a kilometre upstream of this point and no further aquatic molluscs were found.

The Northern Plateau

The area around Malange (3,400 feet) is open savannah with *Brachystegia* woodland. The ground falls slightly towards Duque de Braganza and Pungo Andongo and in both of these areas occasional baobabs are seen near water and the woodland is more dense. There are several moderate-sized rivers in the district (Cuanza, Lucalla, Cole), also smaller rivers and streams. The rivers flow steadily and in places there are sudden drops giving rise to rapids and, in the most extreme case, to the magnificent falls at Duque de Braganza on the Lucalla. In the rivers various prosobranchs are probably common. *Bellamya unicolor* and *Gabbia kisalensis* were found in the Rio Cuije from which von Martens (1882) recorded *Pila ovata*; *Lanistes libycus* was collected in the fringing papyrus swamp of the Lucalla. Welwitsch found *Cleopatra bulimoides* in the streams near Pungo Andongo (Pl. 16, figs. 3, 4) but this species was not seen by me. Where the smaller streams have been dammed or the flow is reduced due to widening of the bed a rich pulmonate fauna is present, *Bulinus globosus*, *B. angolensis*, *Biomphalaria salinarum*, *Gyraulus costulatus* and *Lymnaea natalensis* were all found together in the same place. In very stagnant water *Anisus misellus* and *Bulinus forskali* were found and in an apparently temporary shallow, swampy pool *B. scalaris* and *B. globosus* were collected.

Welwitsch obtained *Succinea badia* Morelet on islands in the Rio Cuanza but these were not visited by me and I saw no sign of members of this genus in the area. Despite a careful search of several streams in the neighbourhood of the Pedras Negras, an impressive chain of hills of a dark, conglomerate rock in the area of Pungo Andongo, no freshwater molluscs were found in what often seemed to be almost ideal conditions. The Pedras Negras are rich in minerals particularly manganese, and it is possible that a high concentration of these minerals in the streams makes them unsuitable habitats for snails.

The Southern Plateau

The Ganguelas district in the North-eastern part of Huila Province has a fairly uniform altitude of about 5,000 feet. The country is gently undulating savannah with patches of *Brachystegia* and mopane woodland, ground orchids are common in damp places and the climate is distinctly cooler than in the three other areas so far described. The principal rivers flow roughly north to south and their tributaries run east-west. In many places it is difficult to decide during the dry season which way the water might flow in the rains because the watersheds are so poorly defined. The rivers on the western side of the district all flow into the Cunene which enters the Atlantic Ocean on the border between Angola and South-west Africa while those on the eastern boundary form part of the Cubango system running south-eastward to drain into the Okavango swamp and Lake Ngami. It is probable that Lake Ngami had relatively recent connections with the Zambesi drainage but Pilsbry and Bequaert's (1927) map indicating the hypothetical extent and distribution of lake and river basins in Africa towards the end of the Pleistocene era also suggests a connection with the Limpopo system.

Because of the terrain in the Ganguelas district the rivers were not fast-flowing at the time of my visit (at the beginning of the rainy season) and many of the smaller tributaries were no more than chains of pools in otherwise practically dry beds. These habitats are ideal for several pulmonate species and in most of them *Bulinus africanus*, *B. angolensis*, *Biomphalaria pfeifferi* and *Lymnaea natalensis* were found, often in considerable numbers, and *Gyraulus costulatus* was usually also present. A second type of habitat in several places (Cassinde Pequeno is the best example) results largely from human activity; in some of the villages where there is no convenient natural water point a type of open well (caçimba) is dug on a sloping hill-side. Water seeps into the pit and the surplus runs off down the slope where it accumulates in small pools, often only a foot or two across and a few inches deep, and in these *Bulinus africanus* and *Lymnaea natalensis* are common. The irrigation system of the Granja Administrativa near Quesso provides an excellent habitat for *Bulinus africanus*, *Biomphalaria pfeifferi* and *Lymnaea natalensis* all of which were found in the main irrigation furrow. It is interesting that the only indication of the presence of prosobranchs in this area came from a single shell of *Melanoides tuberculata* found at the intake of the irrigation system by Dr. Guedes de Carvalho about a month before my visit. Despite searches in some of the large rivers no other operculates were found but Haas (1934) described *Bellamya monardi* from the Rio Kilui (? = *Cului*) and the Cunene near Mulondo and Connolly (1930)

reported *Melanoides victoriae* (= *tuberculata*) from the Cunene as well as *Pila occidentalis* which was originally described from the river by Mousson (1887) and was later reported again by Adensamer (1929). Connolly (1930) also lists a number of prosobranchs collected from the Okavango system (the lower part of the Cubango) by Shortridge and others. Connolly notes that with the exception of *Pila wernei* and *Viviparus leopoldvillensis* all of the gastropods collected by Shortridge were bleached but despite this he believes that they are all still living in the Omuramba-Omatake river which is a tributary of the Okavango.

General Discussion

From this regional account several significant facts concerning the distribution of the freshwater gastropod fauna have emerged. Reference to the table shows that there is only a single species common to all four of the areas visited, namely *Lymnaea natalensis*. This species is widely distributed all over the continent and, although there is considerable local variation, it does not appear to have undergone any distinct speciation. Despite the usually fragile shell and poor ability of the adult snails to withstand desiccation, the species must have characteristics favouring rapid dispersal. The poor differentiation of local forms suggest that *L. natalensis* may be a relatively recent element in the Ethiopian fauna. Apart from *L. natalensis* the only other species which has been found in the coastal plain around Luanda and in the southern plateau region is *Melanoides tuberculata*, the only prosobranch collected in the Ganguelas district despite relatively abundant records of operculates a little further south. Prosobranchs are usually not found in the upland areas of Africa, they are rare on the high veldt of Southern Rhodesia and absent from the highland area of Ethiopia (Wright and Brown, 1962) and it is probable that the Ganguelas district lies near to the altitudinal limits of most prosobranchs in that latitude. The absence of members of the *Bulinus forskali* species group from Ganguelas may be explained in the same way for Connolly (1930) records *B. forskali* from Mafa, north of Ondongua and from Ondongua itself. These local differences in the freshwater faunas of South-west Africa and the Ganguelas region are particularly interesting in the light of Connolly's (1930) comment that there are no species of land snail known to be common to both South-west Africa and Angola.

Two characteristic elements of the plateau fauna both in the north and the south which are missing from the coastal plain are *Bulinus angolensis* and the genus *Biomphalaria*, both are more abundant in the south and are reputed to be common in the central plateau and the Bailundo highlands. *B. angolensis* has already been discussed in the taxonomic section of this paper but *Biomphalaria* is deserving of more attention. Even the limited amount of material of this genus which has been available for study has shown that there is a marked degree of variation between populations in the Angolan region. I have suggested (Wright 1961) that such increased variation in part of the range of a species or species complex may indicate the area in which that species has evolved and I used the complicated situation in the *Bulinus africanus* group in Southern Tanganyika to provide an illustration of this hypothesis. It may be that here in Angola is the original area from which the genus *Biomphalaria* has radiated out.

The distribution of the "small planorbids" shows some apparently characteristic features. *Lentorbis* and *Segmentorbis* were found only in the coastal plain, usually in rather stagnant water, where *Anisus misellus* is also common, but a single sample of this species from the northern plateau indicates its greater range, and if it is the same species as the form recorded under the name *Planorbis gibbonsi* by Connolly (1930), it occurs also in South-west Angola. *Gyraulus costulatus* on the other hand is common in the southern plateau region and has also been found in one locality in the Malange area and one in the escarpment zone, but not together with *A. misellus*. It was suggested in the taxonomic section dealing with *Bulinus africanus* that this species reached southern Angola through the Lake Ngami-Okavango system and it is possible that *Gyraulus costulatus* came the same way and has since spread northward across the Bailundo highlands watershed. *Anisus misellus*, with its close affinities to the west African species referred to *Gyraulus gibbonsi* by Binder (1958), appears to represent (together with *Bulinus truncatus rohlfsi*) a genuinely West African element which has spread southward down the west coast.

The route suggested for the arrival of *Bulinus globosus* in the coastal plain from Tanganyika by way of Northern Rhodesia and Katanga may have been that by which *B. scalaris* and *B. forskali* also entered Angola although *B. forskali* probably arrived earlier than *B. globosus*. *B. crystallinus* may be either a specialised local form evolved in the unfavourable conditions of the forested slopes of the escarpment zone or it may represent a relic of an ancestral form of the *forskali* group whose distribution was wider when the great rain forests covered a much larger area of the continent than they do now. It would be interesting to make a close comparison between *B. crystallinus* and the superficially similar *B. camerunensis* Mandahl-Barth, 1957b, for there is a strong possibility that this species, known only from a crater lake in the Cameroons, may also be an isolated relic of the ancestral form of the *forskali* complex.

To note the presence of certain species in some areas and to suggest how they got there is not enough. It is necessary to try to define the factors which limit the present distribution patterns, if they are in fact limited. The factors are climatic and topographic but it is seldom possible to determine the exact limiting values of any ecological factor because of the interaction between them. In general terms it is probably correct to say that the genus *Biomphalaria* is confined to the Angolan plateau and is absent from the escarpment and coastal plain because the species concerned tend to favour a cooler climate and gently flowing but not turbulent water. The same is true for *Gyraulus costulatus* but in this species the limits of tolerance of water velocity are probably higher, whereas in *Anisus misellus* the opposite conditions seem to be the most favourable. There are undoubtedly many populations of *Burnupia* species in the escarpment region but it is unlikely that they will be found in the coastal plain where the water velocity is less. Harry and Cumbie (1956a/b) have given an excellent illustration of how the effects of topography on stream gradient limit the distribution of *Australorbis glabratus* in Puerto Rico and more recently Scorza et al. (1961) have given a definite limiting value for the factor of water velocity in the distribution of the same species in

Venezuela. The majority of snail habitats in the Angolan coastal plain are in static water while those on the southern plateau are nearly all in water that is either gently flowing throughout the year or periodically flowing, and on the northern plateau there is a mixture of the two general types.

The important climatic factors affecting the distribution of freshwater snails are rainfall and temperature. Rainfall is of direct importance only in that it provides the raw material for bodies of freshwater but it has little or no limiting effect on its own for the porosity of the soil and the topography of the land will determine whether the water is held or not, and the ambient relative humidity will affect evaporation rates and control to some extent the duration of surface water that is retained. Suitable freshwater habitats for snails may be present in areas of low rainfall if the water is provided by rivers (as is the case in the Luanda area of the coastal plain) while steeply sloping areas with high rainfall may not retain enough water to provide habitats. In contrast to rainfall the effects of temperature are direct but not easily measured. It is simple enough to record daily maxima and minima and these are some guide to climate but the upper and lower limiting temperatures governing snail distribution are combined with a time factor. It is possible under laboratory conditions to determine the optimum controlled temperature for breeding of a given snail species and there is a range above and below this optimum within which reproduction can still proceed at a sufficiently high level to maintain the population, provided that the temperature remains within this range for a sufficiently long period. This breeding temperature range is extremely important in determining the distribution of a snail species although there may be cases in which the upper or lower lethal limits of the species' tolerance are involved. Here again there will be a time factor and it is only by experiment that these limits can be worked out. Many African species can withstand temperatures near freezing point for a short period but repeated exposure to such conditions will result in death.

The general picture, then, of the Angolan freshwater gastropod fauna is of two main groups, one composed of species favouring the static water and relatively high temperatures of the coastal plain, the other formed by species preferring the moving waters and lower temperatures of the southern plateau. The elements in each of these groups are probably derived from different geographical origins but the continued separation of the groups is maintained by topographic and climatic differences. In the northern plateau there exist physical conditions within the tolerance of both groups and here the ranges of some of the species overlap. The escarpment fauna is probably rather specialised but where conditions permit there are intrusions from either the coastal plain or the plateau.

ANGOLAN MOLLUSCS OF MEDICAL AND VETERINARY IMPORTANCE

Because this work is connected with a larger study of African molluscs of medical and veterinary importance it is appropriate to include some mention of the economic significance of certain species discussed above as well as the ecology of the transmission cycle of human schistosomiasis in some areas.

Two general reviews have emphasized the widespread incidence of *Schistosoma haematobium* in Angola (Gillet, 1956, Janz and Carvalho, 1956) ; both also mention the scarcity of *Schistosoma mansoni* and the high infection rate in cattle with *S. bovis*.

The earliest quoted record of identified urinary schistosomiasis in Angola is in 1896 and since then records have been gradually accumulating and detailed surveys of a number of areas have been undertaken. Mesquita (1952b) lists the recorded infection rates in twelve localities from all over the territory ; they vary from 16 per cent. at Ambriz to 66 per cent. in Ganguelas and the mean for the twelve sets of figures is just over 40 per cent. Ferreira (1953) in a more general review of disease in Angola noted that the principal foci of urinary schistosomiasis are at Malange, Catete, Caxito, Vila de Ponte and Quilengues, the first in the northern plateau region, the next two on the coastal plain and the other two on the southern plateau. Ferreira also commented on the reduced rate in the central region.

It is fortunate that figures for the incidence of *Schistosoma haematobium* are available for most of the areas in which my collections were made and it is therefore possible to deal with each of the regions in turn.

Coastal Plain. In the Catete area Janz and Carvalho (1956) reported an infection rate of 63.5 per cent. in 1,445 children under fifteen years old and 85.2 per cent. in 889 adults. The rates were equal in children of both sexes and slightly higher in adult men than women. Gillet (loc. cit.) quotes the medical officer of the Fazenda Tentativa sugar plantation as saying that most of the workers on the Fazenda have the infection and Mesquita (1952b) gives the overall infection rate for the Dande area (which includes Fazenda Tentativa) as 61 per cent. These high figures suggest that there is frequent contact with water by the human population and throughout the area *Bulinus globosus* is one of the dominant snail species. The relationship between irrigation and schistosomiasis is too well known for the situation at Fazenda Tentativa to require elaboration. Janz and Carvalho (1956) have suggested that there is a tendency for villages in arid areas to be concentrated near to permanent sources of water and in the Catete region this means the large, shallow lakes near the Cuanza and Bengo rivers. In these lakes there are enormous populations of *Bulinus globosus* and the snails are particularly abundant near to points of human contact. Towards the end of the dry season when the water is low the snail populations are relatively even more dense and it is probably at this time that transmission is at its peak. It is assumed that the form of urinary schistosomiasis in the area is that carried by *Bulinus globosus* but the presence of *B. truncatus rohlfsi* in at least two of the lakes means that conditions for the successful establishment of the "Mediterranean" form of the parasite are available since it has been shown by laboratory experiments (mentioned in the taxonomic section) that this species of snail from Lagoa Cabemba is susceptible to both the Cairo and Khartoum strains of *S. haematobium*.

The Escarpment Zone. Casaca and Carvalho (1955) surveyed the area around Salazar and examined 250 children under fifteen in whom they found an infection rate of 39.7 per cent. in boys and 56.3 per cent. in girls. They also examined 250

adults of which 7.1 per cent. of the men and 34.3 per cent. of the women were passing eggs. The authors searched many streams and rivers in the area and found only snails which they refer to as *Phisa* spp. (probably *B. crystallinus*) except in the Rio Moembege where they found large numbers of *Bulinus globosus* and *Lymnaea natalensis*, also a single *Biomphalaria pfeifferi*. By crushing the snails the authors claim to have found 70 per cent. of the *B. globosus* to be infected with larval schistosomes and 10 per cent. of the "*Phisa* spp." but these figures are exceptionally high and probably include a number of cases of non-pathogenic trematodes. There is no doubt, however, that here the principal intermediate host for *S. haematobium* is *B. globosus* for Casaca and Carvalho found that the species was limited to a certain polluted area of the Rio Moembege and that the overall infection rates in children in sections of the town and its surrounding villages were proportional to their proximity to the heavily snail-infested part of the river. Thus in the district of Alto da Rosa immediately bordering the dirty part of the stream the rate was 85.2 per cent. while in Cassuala and Quifué which are a little further away but draw their water from the same part of the river the rates were 72.7 and 69.2 per cent. respectively. At Quilombo on a clean part of the river downstream from Alto da Rosa the rate was 50 per cent. and in Coqueiros, Camundai and Bandeira on tributaries of the Moembege where only "*Phisa* spp." were found the rates were 44, 24 and 24 per cent. and at Quihanda on a tributary in which no snails were present no cases were found. The evidence suggesting that *Bulinus crystallinus* is transmitting *S. haematobium* is important because it adds another intermediate host to the members of the *forskali* group whose role is so often the subject of discussion. The other point of interest in the observations of Casaca and Carvalho is the limited occurrence of *B. globosus* in the district, confirming that it is not truly a species of the escarpment zone but is only able to exist where changes in stream gradient and openings in the forest provide the necessary conditions of slow-moving water and adequate sunlight. It seems probable that schistosomiasis is of only local importance in the escarpment zone.

The Northern Plateau. Mesquita (1952b) reported a general infection rate of 65 per cent. in Malange and 31 per cent. at Duque de Braganza. Ferreira and Gomes (1959) examined 27,577 urine samples in the Malange district and found an overall rate of 43 per cent. with heavily infected foci at Xa Muteba (5 de Outubro) and Bangale (81 and 70 per cent.) and the lowest incidence at Duque de Braganza with 24 per cent.

Neither of these papers includes information on transmission and my own work in the district was not sufficiently extensive. The rivers are unlikely to be important sources of infection but the temporary pools and small streams, especially where they have been dammed for agriculture or fish-keeping are the most frequent habitats for *Bulinus globosus* and are therefore the potential danger points.

The Southern Plateau. My visit to this area was made possible by the Angolan Medical Services for whom I prepared a brief report on the snail fauna of the Ganguelas district and its probable significance in the transmission of schistosomiasis. Since that report was submitted a urine survey of many of the villages in the area has

been carried out (Guedes de Carvalho, 1959) and much of this section is based on my original report and its interpretation in the light of that survey.

Urinary schistosomiasis has been known to occur in Huila Province since 1902 when, according to Janz and Carvalho (1956), the first case was reported by Bernadino Roque. In 1939 a survey of the district around Cuchi was made by Sarmento (1944). Cuchi is in Bié Province but it is particularly relevant to this account because it adjoins Ganguelas on the east side of the Rio Cutato. Sarmento found 60.2 per cent. of the children and 21.5 per cent. of the adults infected and he noted that the incidence was higher in women than men. Cambournac, Gandara and Pena (1955) also surveyed Cuchi and the two districts to the east of it, Menongue and Longa. In Longa the overall incidence was only 3.3 per cent. but in Cuchi and Menongue the rates were much higher (42.3 and 51.6 per cent.). In both areas about half of the children were found to be infected and there was little difference in the rate between the sexes but the percentage of adult females passing eggs was significantly higher than the rate in men. The area is populated largely by two tribes, the Ganguelas and the Quiocos, the Ganguelas are said to be the more primitive of the two and they have a slightly higher infection rate. Two surveys to the west of Ganguelas (Cambournac, Gandara and Casaca, 1956 and Cambournac and Casaca, 1956) provide further information on local infection rates. At Capelongo 13.8 per cent. of 500 people examined were infected, the rate in adult women was again higher than in men, and at Mulondo a 12.9 per cent. rate was detected in 200 children under fifteen years old and 11 per cent. in 800 adults with the rates higher in male children and female adults.

In Guedes de Carvalho's (1959) survey of villages in the Ganguelas district a single urine sample was taken from 35 children between the ages of three and fourteen in each village except where there were less than 35 in a village and in these cases all of the children were examined. In the light of the results from neighbouring districts where a higher rate was found in children than in adults it is likely that the percentage rates given by Carvalho for the villages are greater than the true overall rates. Carvalho gives no figures for the main town of Vila Artur de Paiva but Janz and Carvalho (1956) quote 70 per cent. for a sample of 150 boys and this rate can be considered to be comparable with those given by Carvalho. Only the information relevant to villages whose water supply was examined by me for snails will be considered here.

At Capemba and San José *Bulinus africanus* is common in shallow pools of a hill-side seepage forming the source of a small stream and the infection rates are 57 per cent. for Capemba and 66.6 per cent. for San José. Cassinde Pequeno is close to these two villages and the snail habitat is similar but derived from the excess run-off from a caçimba, here the infection rate is 74.3 per cent. Quesso is the village nearest to the Granja Administrativa and it is probable that the 45.7 per cent. infection rate has its origins in the farm irrigation system although *Bulinus africanus* is common in the marshy ground near to the river bank. Catoco is interesting in that the villagers claim to use the Rio Cubango as their source of water and if this is the case the infection rate in the children should be low because the river does not

provide suitable snail habitats. However, the local fear of crocodiles is such that it is most unlikely that they bathe at the point shown to me and a chain of pools in a stream-bed near the village is a much more likely bathing place. These pools are well populated with several snail species including *B. africanus* and the recorded infection incidence of 62.8 per cent. seems to indicate that this is the main transmission point. At Cangombe the heavily snail-infested stream passes through native gardens from which rubbish is dumped into it, and it is also used for washing and bathing. Under these circumstances the 66.6 per cent. infection rate seems low. The stream at Senga passes right beside the village and in it all of the freshwater snail species of the Ganguelas district occur. The stream is used for washing and bathing and the 77.1 per cent. recorded incidence is not surprising. At Gunda Vunjanga the fear of crocodiles prevents the inhabitants from using the nearby Rio Cutato and instead they draw their water from and bathe in a deep pool in a stream bed in which *B. africanus* occurs. In my report I anticipated a high infection rate in this village and this is confirmed by Carvalho's figure of 86.6 per cent. The results of the urine survey at Indungo have provided the greatest surprise, for here the domestic water supply is obtained from seepage pits dug in a wide area of vlie surrounding a small stream bed. No snails were found in either the stream or the pits and the infection rate of 45.7 per cent. suggests that the inhabitants go to some more distant place to bathe.

Two important facts emerge from this survey. The first is the significant part played by the local fear of crocodiles which prevents the inhabitants of many villages from using the relatively snail-free rivers for bathing and causes them to resort to small streams and pools in which *Bulinus africanus* is nearly always present, often in large numbers. Although the only area in which I was aware of this marked fear of crocodiles was in the Ganguelas district, it is undoubtedly widespread; Livingstone (1857) noted that on the banks of the Lucalla river there were various devices to enable the inhabitants to draw water without coming too close to it themselves. The second important fact in the Ganguelas district is that throughout the area examined the transmission foci are usually well-defined and easy to locate. This should facilitate the problem of control but it is clear that any mollusciciding work will have to be repeated regularly because *B. africanus* is common everywhere in the district and repopulation of treated places is likely to occur rapidly.

The problem of *Schistosoma mansoni* in Angola is exceptionally interesting. Mesquita (1952a) reported two cases in the Malange district, both in individuals who were said not to have left the area but despite repeated surveys for intestinal parasites no other cases were reported until one was diagnosed in Benguela in a native from the Moxico area. As a result of this finding a large survey was carried out in Alto Zambeze (Janz and Carvalho, 1957) and a 1.1 per cent. infection rate was found in over 2,000 individuals examined.

Throughout the plateau region snails of the intermediate host genus *Biomphalaria* are found and it is difficult to believe that they are all resistant to infection with *S. mansoni*. *B. pfeifferi* which is common in Huila Province is certainly known to be a successful host in other parts of Africa and it seems that the only possible

explanation is that the parasite has not yet been introduced into the area. With increased movement of Africans as communications in the continent improve it is very likely that intestinal schistosomiasis will eventually become established at least in some parts of the Angolan plateau.

Information about parasites of cattle in Angola is not available apart from Gillet's (loc. cit.) mention of the finding of *Schistosoma bovis* in the mesenteric plexus of eight out of ten cattle from Bom Jesus which were examined in the abattoir at Luanda and Janz and Carvalho's (1956) report of the eggs of *S. bovis* in the faeces of 78.1 per cent. of 258 cattle at Bom Jesus. These last authors also examined the faeces of 33 goats, sheep and pigs in the same area but without success. The cattle ranch at Bom Jesus receives stock from many parts of the territory and the origin of the cases reported is therefore uncertain but it is probable that the parasite is widespread. The intermediate hosts for *S. bovis* are the same as those for *S. haematobium*. The wide distribution and abundance of *Lymnaea natalensis* and the presence of larval forms of the cattle liver fluke *Fasciola gigantica* in many of the specimens examined makes it probable that this parasite is widespread in Angola. The finding of amphistome cercariae in specimens of *Bulinus angolensis* suggests that these flukes too are likely to be widespread at least in the plateau region.

ALPHABETICAL LIST OF COLLECTING PLACES

1. Bom Jesus, Luanda Province. 9° 09' S., 13° 34' E. Small lake on the banks of the Rio Cuanza, contained only a few inches of stagnant water when visited on 13th November, 1957. *Anisus misellus*, *Bulinus globosus*, *B. forskali*.

2. Cabemba (Lagoa), Luanda Province. 9° 18' S., 13° 55' E. Large lake on the flood plain of the Rio Cuanza. The point visited was a muddy sand beach near a fishing settlement. There was emergent grass at both ends of the beach and a floating island of vegetation about half a mile off-shore. Snails were collected on *Ceratophyllum* sp. in about one foot of water off the beach. 14th November, 1957. *Bulinus truncatus rohlfsi* and *B. forskali*.

3. Cabungabunga (Lagoa), Luanda Province. 9° 07' S., 13° 44' E. Lake on the flood plain of the Rio Cuanza on the road from Catete to Muxima. Point visited was a large pool on the edge of the main lake, lily-covered and with thick black mud bottom. 13th November, 1957. *Bulinus globosus* and *B. forskali*.

4. Cangombe, Huila Province. 14° 27' S., 16° 14' E. Village about four kilometres from Vila Artur de Paiva on Galangue road. Snails collected from a chain of pools in an almost stationary stream passing through native gardens just below the washing place. 21st November, 1957. *Biomphalaria pfeifferi*, *Gyraulus costulatus*, *Bulinus africanus*, *B. angolensis* and *Lymnaea natalensis*.

5. Capembe and San José, Huila Province. 14° 20' S., 16° 14' E. Twin villages sharing a water point about eight kilometres from Vila Artur de Paiva on the Galangue road. Water drawn from a seepage ditch cut in the hillside below the villages. The ditch is the beginning of a small stream flowing into the Rio Cubango. 21st November, 1957. *Bulinus africanus* and *Lymnaea natalensis*.

6. Cassinde Pequeno, Huila Province. $14^{\circ} 22' \text{ S.}, 16^{\circ} 17' \text{ E.}$ Village about nine kilometres from Vila Artur de Paiva on Galange road. Water point a half open well (caçimba) on the hillside into which water seeps and the surplus runs off in a trickle forming pools in which snails were common. 21st November, 1957. *Bulinus africanus* and *Lymnaea natalensis*.

7. Cassinga, Huila Province. $15^{\circ} 08' \text{ S.}, 16^{\circ} 05' \text{ E.}$ Village about 90 kilometres south of Vila Artur de Paiva. Waterpoint in a backwater of the Rio Cului, near the ford. Snails scarce and small. 22nd November, 1957. *Bulinus africanus* and *Lymnaea natalensis*.

8. Cativa, Huila Province. $14^{\circ} 10' \text{ S.}, 16^{\circ} 12' \text{ E.}$ Village about 45 kilometres north of Vila Artur de Paiva on track leading from Galangue road. Water point in Rio Cuando, slow moving tributary of Rio Cubango. Snails not numerous, but present on broad-leaved aquatic plants. 23rd November, 1957. *Biomphalaria pfeifferi*, *Gyraulus costulatus*, *Bulinus africanus* and *Lymnaea natalensis*.

9. Catoco, Huila Province. $14^{\circ} 36' \text{ S.}, 16^{\circ} 24' \text{ E.}$ Village about 12 kilometres south south-east of Vila Artur de Paiva, not in the position shown on the 1 : 1,500,000 Carta de Angola (1935). Water point reputed to be in Rio Cubango but this is unlikely to be a bathing place because of the fear of crocodiles. In a shallow valley on the Vila Artur de Paiva side of the village there were pools in a stream bed and snails were plentiful here. 21st November, 1957. *Bulinus africanus*, *B. angolensis* and *Lymnaea natalensis*.

10. Cuije (Rio), Malange Province. $9^{\circ} 35' \text{ S.}, 16^{\circ} 25' \text{ E.}$ Moderate sized river, very muddy and at low water when visited, 24th October, 1957, tributary of the Rio Cuanza. Searched on both banks for several hundred yards on either side of the bridge on the Malange-Cangandala road, also pools on the flood plain on the south bank. *Bellamya unicolor* and *Gabbia kisalensis* in the river and *Bulinus forskali* in a pool on the flood plain.

11. Cului (Rio), Huila Province. $14^{\circ} 30' \text{ S.}, 16^{\circ} 01' \text{ E.}$ Almost stagnant pools in the river bed with heavy lily cover and emergent vegetation. Point visited beside bridge on Vila Artur de Paiva-Dongo road. 23rd November, 1957. *Biomphalaria pfeifferi*, *Gyraulus costulatus*, *Bulinus africanus*, *B. angolensis* and *Lymnaea natalensis*.

12. Dalagosa (Lagoa), Luanda Province. $9^{\circ} 07' \text{ S.}, 13^{\circ} 44' \text{ E.}$ Lake near the village of Bazabom, about 18 kilometres from Catete on Muxima road, on flood plain of Rio Cuanza. Water very low and lake greatly contracted at the time of the visit. 13th November, 1957. Thick black mud bottom, some lily cover and *Ceratophyllum* sp. Snails abundant. *Bulinus globosus*, *B. forskali* and *Lanistes ovum*.

13. Dondo, Cuanza Norte Province. $9^{\circ} 38' \text{ S.}, 14^{\circ} 25' \text{ E.}$ Material collected by Dr. Morias de Carvalho from the Rio Mucoso. 3rd July, 1957. *Anisus misellus* and *Bulinus forskali*.

14. Dongo, Huila Province. $14^{\circ} 36' \text{ S.}, 15^{\circ} 48' \text{ E.}$ Village about 80 kilometres west of Vila Artur de Paiva. Water point in the Rio Cubangue which, when visited

was shallow and slow-flowing with large pools on the bank. 23rd November, 1957. *Biomphalaria pfeifferi*, *Gyraulus costulatus*, *Bulinus africanus*, *B. angolensis* and *Lymnaea natalensis*.

15. Guimbe (Lagoa), Luanda Province. 9° 10' S., 13° 40' E. Large lake near Rio Cuanza, shallow, extensive lily cover and many water birds. 13th November, 1957. *Bulinus globosus* and *B. forskali*.

16. Gunda Vunjanga, Huila Province. 14° 39' S., 16° 27' E. Village about 15 kilometres due east of Vila Artur de Paiva. Water point in deep, lily-covered pool in a stream bed. 22nd November, 1957. *Gyraulus costulatus*, *Bulinus africanus* and *Lymnaea natalensis*.

17. Indungo, Huila Province. 14° 48' S., 16° 17' E. Village about 40 kilometres south of Vila Artur de Paiva. Water point consists of a series of seepage pits dug in a meadow. No snails found. 22nd November, 1957.

18. Lalama (Lagoa), Luanda Province. 8° 57' S., 13° 42' E. Reed-fringed lake near the Rio Calucala. 14th November, 1957. *Succinea patentissima*, *Anisus misellus*, *Lentorbis benguelensis*, *Segmentorbis kanisaensis*, *Bulinus globosus*, *B. forskali* and *Lanistes ovum*.

19. Libongo (Fazenda), Luanda Province. 8° 24' S., 13° 24' E. Oil palm plantation near the mouth of the Rio Lifune. Irrigation ditches contained few snails but these exceptionally large. 9th November, 1957. *Bulinus globosus*.

20. Lucala (Rio), Malange Province. 9° 04' S., 16° 11' E. Large river, water low, thick fringing papyrus swamp but main channel fast flowing, point visited just above the Duque de Braganza falls. Pools on mud banks in papyrus swamp examined. 25th October, 1957. *Lanistes libycus*.

21. Lumango (Lagoa), Luanda Province. 8° 52' S., 13° 38' E. Reed-fringed lake near the Rio Bengo. Marginal vegetation too dense for direct approach to open water. Snails collected in gap in reeds where fishing canoes are drawn up. 14th November, 1957. *Succinea patentissima*, *Bulinus globosus* and *B. forskali*.

22. Matoz (Lagoa), Luanda Province. 8° 32' S., 13° 34' E. Small lake on the north side of the Fazenda Tentativa, near the Caxito-Ambriz road. The lake is reputed to harbour an aggressive crocodile and collecting was confined to a drainage ditch beside it. 8th November, 1957. *Bulinus globosus*, *B. forskali* and *Lanistes ovum*.

23. Moembege (Rio), Cuanza Norte Province. 9° 20' S., 14° 52' E. Moderate stream passing through agricultural research station near Salazar. The stream was examined for over a mile of its length but snails were found only in a relatively short stretch near the main buildings. At this point the banks are steep, the water is swift and shaded by heavy growths of bamboo. 29th October, 1957. *Succinea concisa*, *Gyraulus costulatus* and *Burnupia* sp. (c.f. *gordonensis*).

24. Moembege (Rio), (2), 9° 18' S., 14° 54' E. The stream is similar to the descriptions above but much less shaded for most of its length. It was examined from a point about a mile up-stream of Salazar to just below the town and snails were found in a small backwater, also at the washing place in the town. 30th October, 1957. *Bulinus globosus* and *Lymnaea natalensis*. (Dr. Morais de Carvalho

collected the material of *Bulinus crystallinus* described in this paper from the Moembege and its tributaries in September, 1954).

25. Panguila (Lagoa), Luanda Province. $8^{\circ} 42' \text{ S.}, 13^{\circ} 27' \text{ E.}$ Large lake near the mouth of the Rio Bengo, close to the sea. Three places examined on two successive days (8th and 9th November, 1957), the first was near the bridge on the Luanda-Caxito road, the second was a pool on the edge of the lake near the road and the third point was at the north-west corner of the lake. There is emergent grass all along the west shore and considerable lily-cover on the lake itself. *Anisus misellus*, *Lentorbis benguelensis*, *Bulinus globosus*, *B. truncatus rohlfsi*, *B. forskali*, *Lymnaea natalensis* and *Lanistes ovum*.

26. Quequesse (Lagoa), Luanda Province. $9^{\circ} 07' \text{ S.}, 13^{\circ} 44' \text{ E.}$ Grass-choked swampy lake near the village of Bazabom on the Catete-Muxima road. 13th November, 1957. *Succinea patentissima*, *Anisus misellus*, *Segmentorbis kanisaensis*, *Bulinus globosus* and *Lymnaea natalensis*.

27. Quesso (1), Huila Province. $14^{\circ} 22' \text{ S.}, 16^{\circ} 22' \text{ E.}$ Village about seven kilometres north of Vila Artur de Paiva, near intake of the irrigation system of the Granja Administrativa from the Rio Cubango. Dr. Guedes de Carvalho had shells of *Biomphalaria pfeifferi*, *Bulinus africanus*, *Lymnaea natalensis* and a single *Melanoides tuberculata* collected here in October but no snails were found in the same place on 21st November, 1957. Further down the irrigation system the first three species were all found but there was no sign of further *Melanoides*.

28. Quesso (2), Huila Province. $14^{\circ} 22' \text{ S.}, 16^{\circ} 22' \text{ E.}$ Washing place for the village is said to be in the Rio Cubango but this seems a little unlikely. No snails were found in the river itself but in a marsh behind the river bank *Bulinus africanus* was common.

29. Quifangondo, Luanda Province. $8^{\circ} 44' \text{ S.}, 13^{\circ} 27' \text{ E.}$ Floating marsh on the banks of the Rio Bengo near to the village. 16th November, 1957. *Anisus misellus* and *Lentorbis benguelensis*.

30. Quilunda (Lagoa), Luanda Province. $8^{\circ} 50' \text{ S.}, 13^{\circ} 36' \text{ E.}$ Large lake on the banks of Rio Bengo. Point visited at east end of lake near Cabire. Open beach of limestone (?) shingle with few marginal bushes and some emergent grasses. Water open, no lily cover, clean stone bottom. Snails were found among the emergent vegetation and damp flotsam on the beach, the prosobranchs were also crawling on stones at least three to four feet deep. Fishermen on the beach showed me the stomachs of fish packed with *Melanoides*. 14th November, 1957. *Bulinus globosus*, *Bulinus forskali*, *Lanistes ovum* and *Melanoides tuberculata*.

31. Quionqua (1), Malange Province. $9^{\circ} 10' \text{ S.}, 16^{\circ} 12' \text{ E.}$ Marshy roadside pool about two kilometres north of village on road to Duque de Braganza falls. 15th October, 1957. *Bulinus globosus* and *Bulinus scalaris*.

32. Quionqua (2), Malange Province. $9^{\circ} 12' \text{ S.}, 16^{\circ} 12' \text{ E.}$ Small pool about three feet deep, stagnant and foul with thick mud and marsh gas. Snails on emergent grass. 25th October, 1957. *Anisus misellus* and *Bulinus forskali*.

33. Quissol (1), Malange Province. $9^{\circ} 35' \text{ S.}, 16^{\circ} 28' \text{ E.}$ Small stream crossing

the Malange-Nova Gaia road about five kilometres west of Fazenda Quissol. Water shallow, few aquatic plants. 24th October, 1957. *Lymnaea natalensis*.

34. Quissol (2), Malange Province. 9° 35' S., 16° 30' E. Quastimbala stream on edge of Fazenda Quissol. The stream has been dammed to form a pond beside the road. The water is almost still, there is a little lily cover, some reeds and marginal emergent vegetation. 24th October, 1957. *Biomphalaria salinarum*, *Gyraulus costulatus*, *Bulinus globosus*, *B. angolensis* and *Lymnaea natalensis*.

35. Senga, Huila Province. 14° 30' S., 16° 21' E. Village about fourteen kilometres east-south-east of Vila Artur de Paiva. The water point is in a stream (possibly the same as that near Catoco), the water was gently flowing and there was a good deal of aquatic vegetation. 22nd November, 1957. *Biomphalaria* sp., *Gyraulus costulatus*, *Bulinus africanus*, *B. angolensis* and *Lymnaea natalensis*.

36. Tentativa (Fazenda), Luanda Province. 8° 34' S., 13° 35' E. Irrigation system of sugar cane plantation and stream carrying effluent from sugar factory. 8th November, 1957. *Bulinus globosus*, *Lymnaea natalensis*, *Lanistes ovum* and *Melanoides tuberculata* (irrigation ditches only).

37. Vila Artur de Paiva, Huila Province. 14° 28' S., 16° 20' E. Also known as Vila da Ponte. Main town of Ganguelas District. Water source is a spring near the hospital. The spring itself is covered with a concrete housing but the surplus water runs off down a ditch towards the Rio Cubango. 21st November, 1957. *Biomphalaria pfeifferi*, *Bulinus africanus* and *Lymnaea natalensis*.

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PLATE I

- FIGS. 1-6. *Biomphalaria salinarum*, syntypes, B.M. (N.H.) coll. no. 93.2.4.587-9.
FIGS. 7, 8. *B. salinarum*, Quissol, Malange.
FIGS. 9, 10. *Biomphalaria* sp., Senga, Huila.

All figures are $\times 4$ except where stated otherwise.

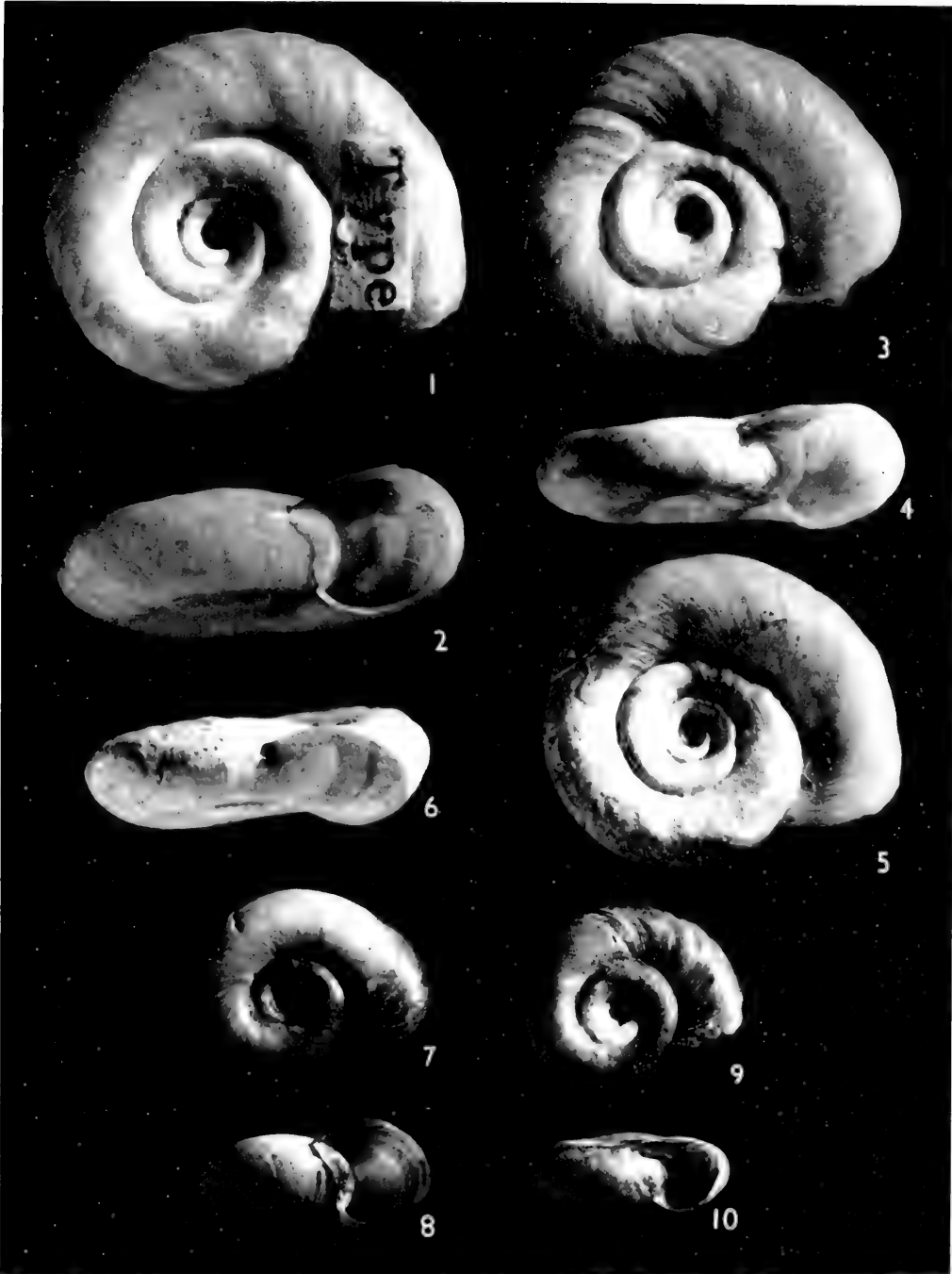


PLATE 2

- FIGS. 1, 2. *Biomphalaria* sp., Nova Lisboa.
FIGS. 3, 4. *B. pfeifferi*, Cangombe, Huila.
FIGS. 5, 6. *B. pfeifferi*, Cativa, Huila.
FIGS. 7, 8. *B. pfeifferi*, Vila Artur de Paiva, Huila.
FIGS. 9, 10. *B. pfeifferi*, Dongo, Huila.
FIGS. 11, 12. *B. pfeifferi*, Rio Cului, Huila.
FIGS. 13, 14. *B. pfeifferi*, Quesso, Huila.



PLATE 3

- FIGS. 1, 2. *Lentorbis junodi*, paratype, showing basal lamella. B.M. (N.H.) coll. no. 1937.12.30.8802.
- FIGS. 3, 4. *L. junodi*, holotype, B.M. (N.H.) coll. no. 1937.12.30.8801.
- FIGS. 5-10. *L. benguelensis*, possible syntypes from Berlin Museum ($\times 5$).
- FIGS. 11, 12. *Segmentorbis kanisaensis*, holotype, B.M. (N.H.) coll. no. 1923.6.8.1224.
- FIGS. 13, 14. *S. kanisaensis*, paratype, B.M. (N.H.) coll. no. 1923.6.8.1925.
- FIGS. 15, 16. *Lentorbis benguelensis* Lagoa Lalama, Luanda.
- FIGS. 17, 18. *Segmentorbis kanisaensis* Lagoa Lalama, Luanda.
- FIGS. 19-24. *Anisus misellus*, syntypes, B.M. (N.H.) coll. no. 93.2.4.590-4.
- FIGS. 25, 26. *Anisus misellus*, Quifangondo, Luanda.
- FIGS. 27, 28. *Gyraulus costulatus*, Rio Moembege, Cuanza Norte.
- FIGS. 29, 30. *G. costulatus*, Rio Cului, Huila.

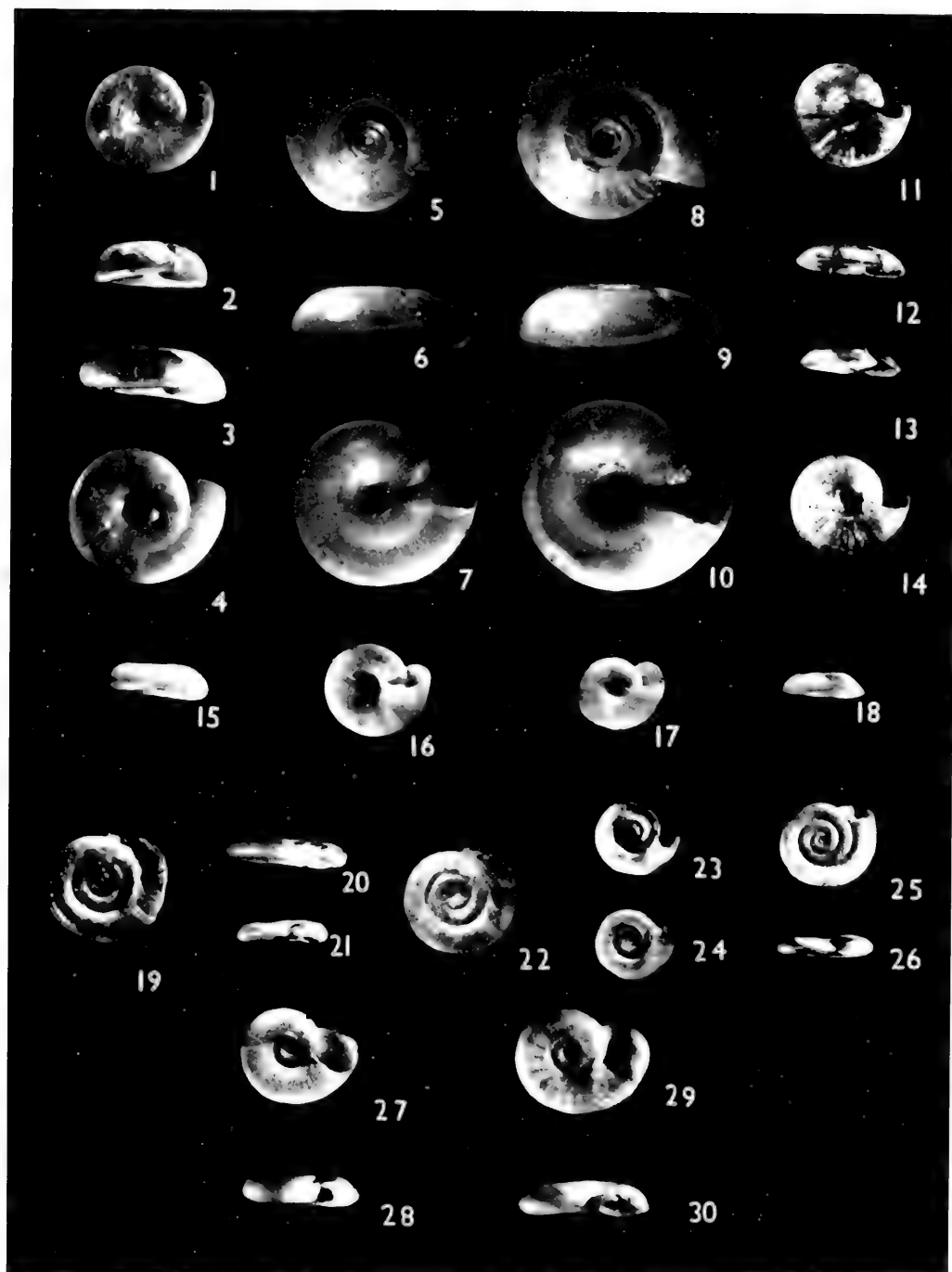


PLATE 4

- FIG. 1. *Bulinus globosus*, Lagoa Matoz, Luanda.
FIG. 2. *Bulinus globosus*, Fazenda Libongo, Luanda.
FIG. 3. *Bulinus globosus*, Fazenda Tentativa, Luanda.
FIG. 4. *Bulinus globosus*, Lagoa Dalagosa, Luanda.
FIG. 5. *Bulinus globosus*, Lagoa Quilunda, Luanda.
FIG. 6. *Bulinus africanus*, Cassinde Pequeno, Huila.
FIG. 7. *Bulinus africanus*, Cangombe, Huila.
FIG. 8. *Bulinus africanus*, Quesso, Huila.

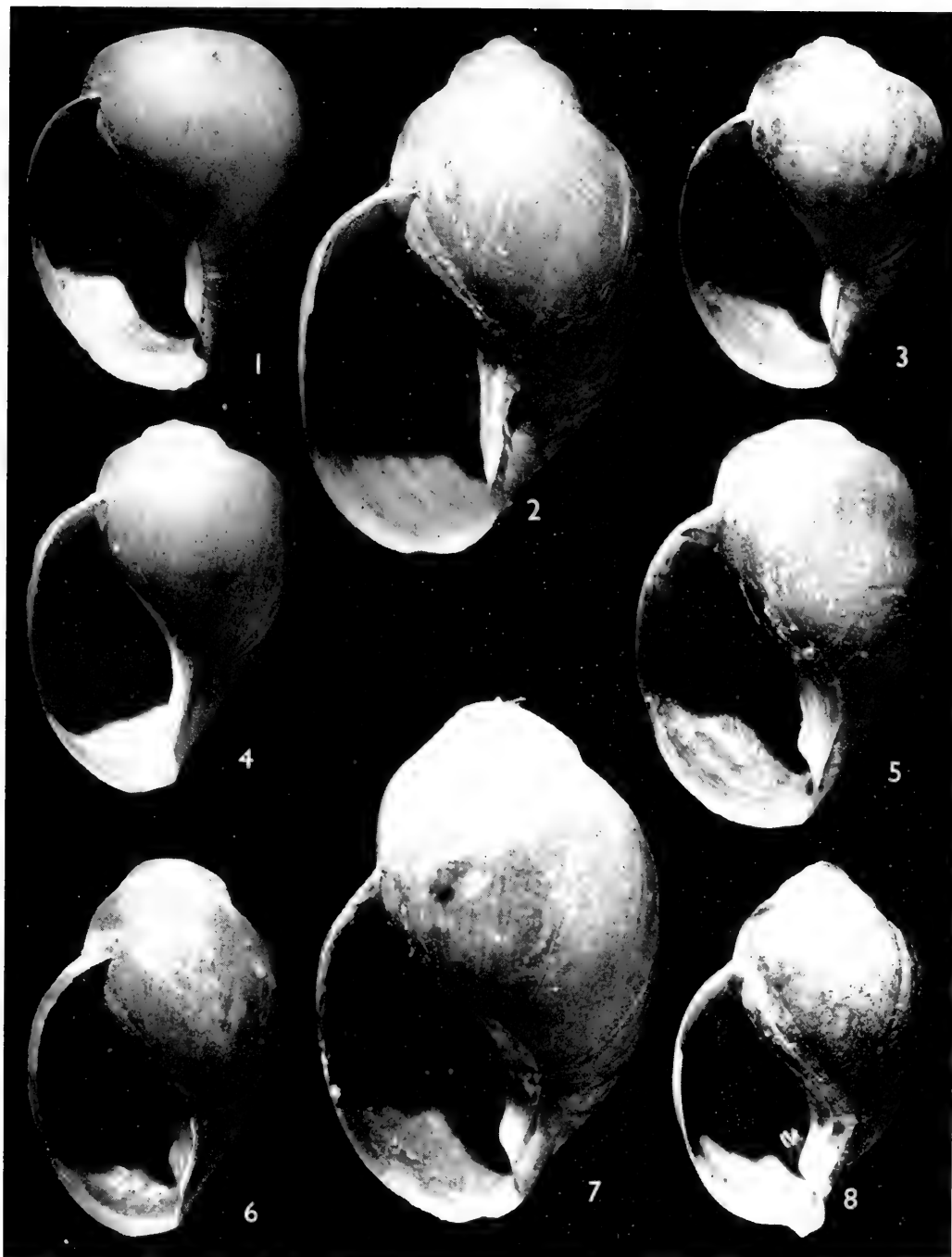


PLATE 5

- FIG. 1. *Bulinus angolensis*, Cangombe, Huila.
FIG. 2. *B. angolensis*, Rio Cului, Huila.
FIG. 3. *B. angolensis*, Catoco, Huila.
FIG. 4. *B. angolensis*, Quissol, Malange.
FIG. 5. *B. angolensis*, Dongo, Huila.
FIG. 6. *B. globosus*, holotype, B.M. (N.H.) coll. no. 93.2.4.681.
FIG. 7. *B. globosus*, paratype, B.M. (N.H.) coll. no. 93.2.4.682.

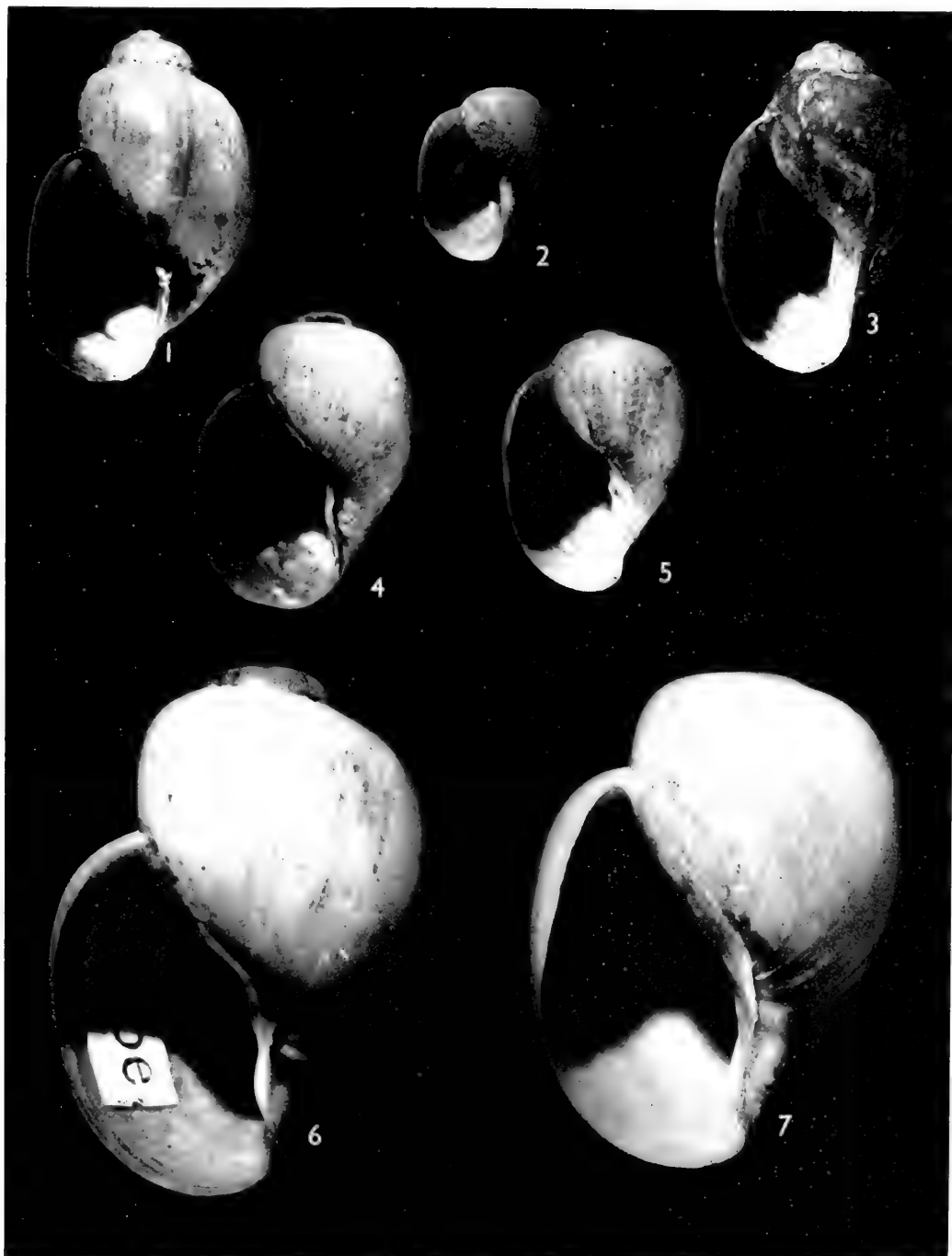


PLATE 6

Bulinus angolensis

FIGS. 1-3. *B. welwitschi*, syntypes, B.M. (N.H.) coll. no. 93.2.4.615-17.
FIGS. 4, 5. *B. angolensis*, syntypes, B.M. (N.H.) coll. no. 93.2.4.618-19.

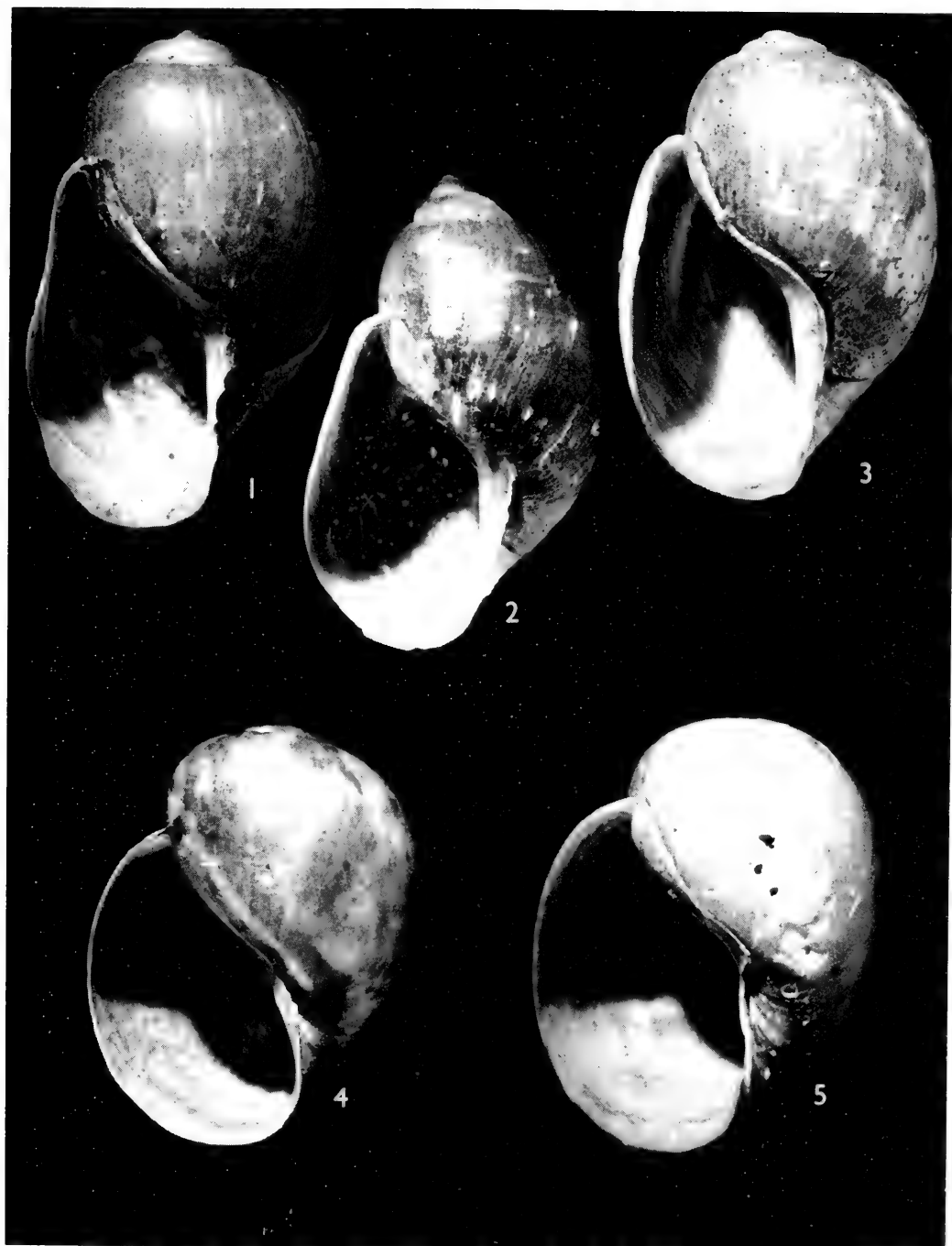


PLATE 7

Bulinus forskali.

- FIGS. 1-3. *B. schmidtii*, syntypes, Berlin Museum.
FIGS. 4, 5. *B. capillacea*, syntypes, B.M. (N.H.) coll. no. 93.2.4.654-5.
FIGS. 6-9. *B. apiculata*, syntypes, B.M. (N.H.) coll. no. 93.2.4.647-50.
FIG. 10. *B. turriculata*, holotype, B.M. (N.H.) coll. no. 93.2.4.505.
FIGS. 11-14. *B. clavulata*, syntypes, B.M. (N.H.) coll. no. 93.2.4.643-6.
FIGS. 15-17. *B. semiplicata*, syntypes, B.M. (N.H.) coll. no. 93.2.4.621-3.

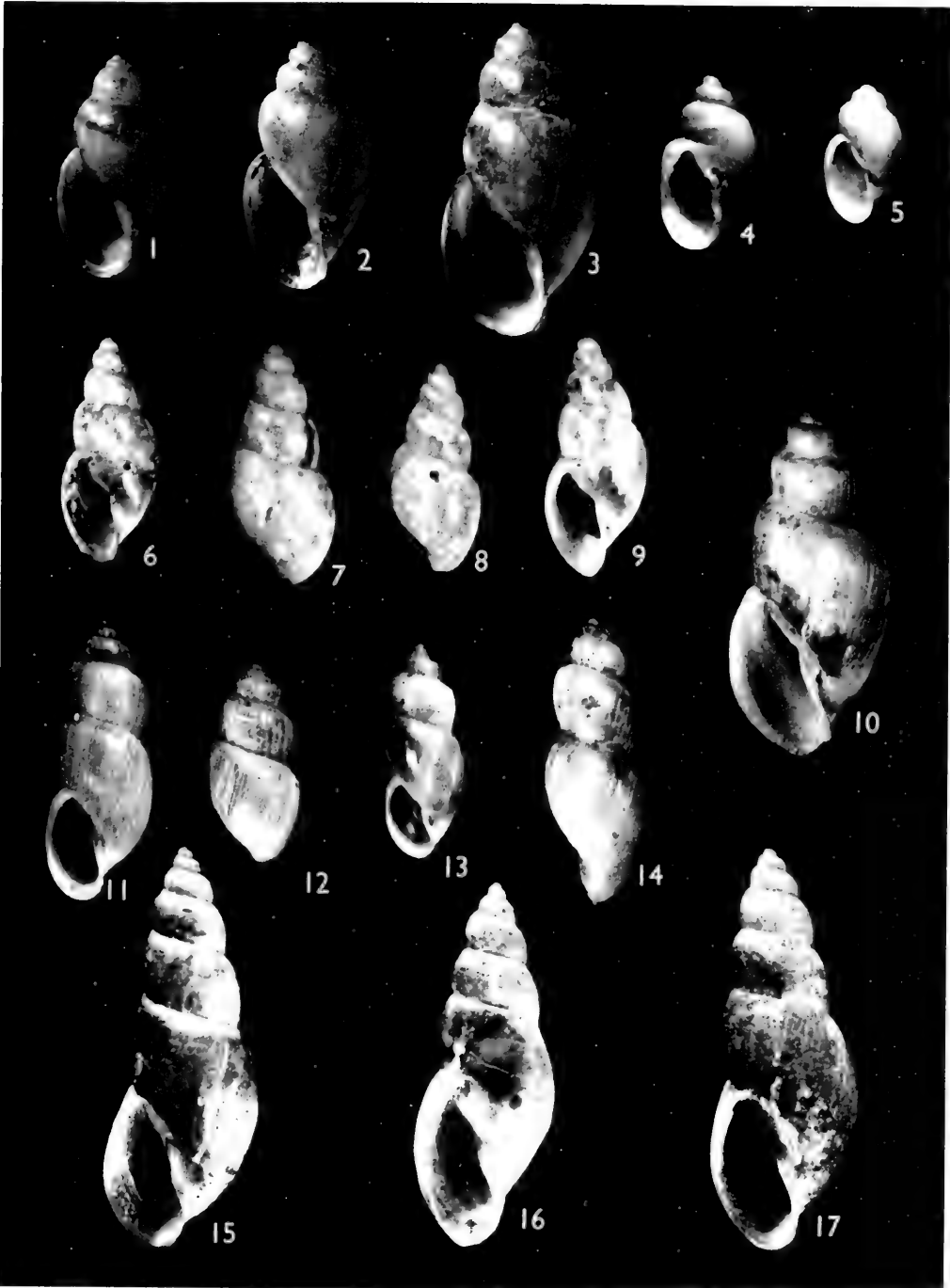


PLATE 8

- FIGS. 1-6. *Bulinus forskali*, laboratory bred from a stock originating from Lagoa Panguila, Luanda.
- FIGS. 7, 8. *B. forskali*, Lagoa Lalama, Luanda.
- FIGS. 9-11. *B. forskali*, Lagoa Cabungabunga, Luanda.
- FIGS. 12-14. *B. forskali*, Dongo, Cuanza, Sul.
- FIGS. 15, 16. *B. forskali*, Lagoa Dalagosa, Luanda.
- FIGS. 17-19. *Burnupia* sp. (c.f. *gordonensis*) Rio Moembege, Cuanza Norte.
- FIGS. 20-22. *Burnupia gordonensis*, holotype, B.M. (N.H.) coll. no. 1904.4.29.40.

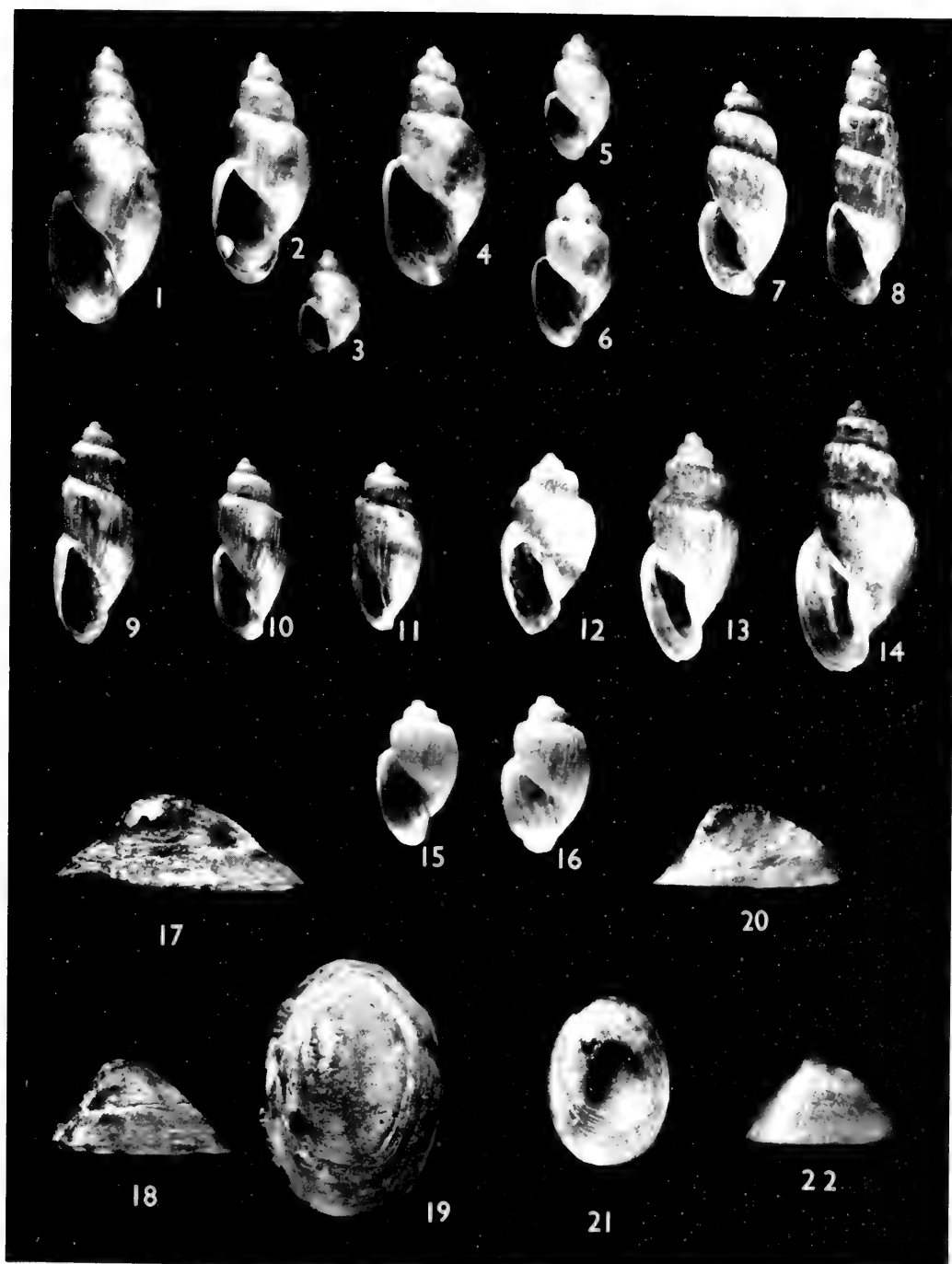


PLATE 9

Bulinus scalaris

- FIGS. 1-3. *B. scalaris*, syntypes, Berlin Museum.
FIGS. 4-6. *B. benguelensis*, syntypes, B.M. (N.H.) coll. no. 196280.
FIGS. 7, 8. *B. canescens*, syntypes, B.M. (N.H.) coll. no. 93.2.4.606-7.

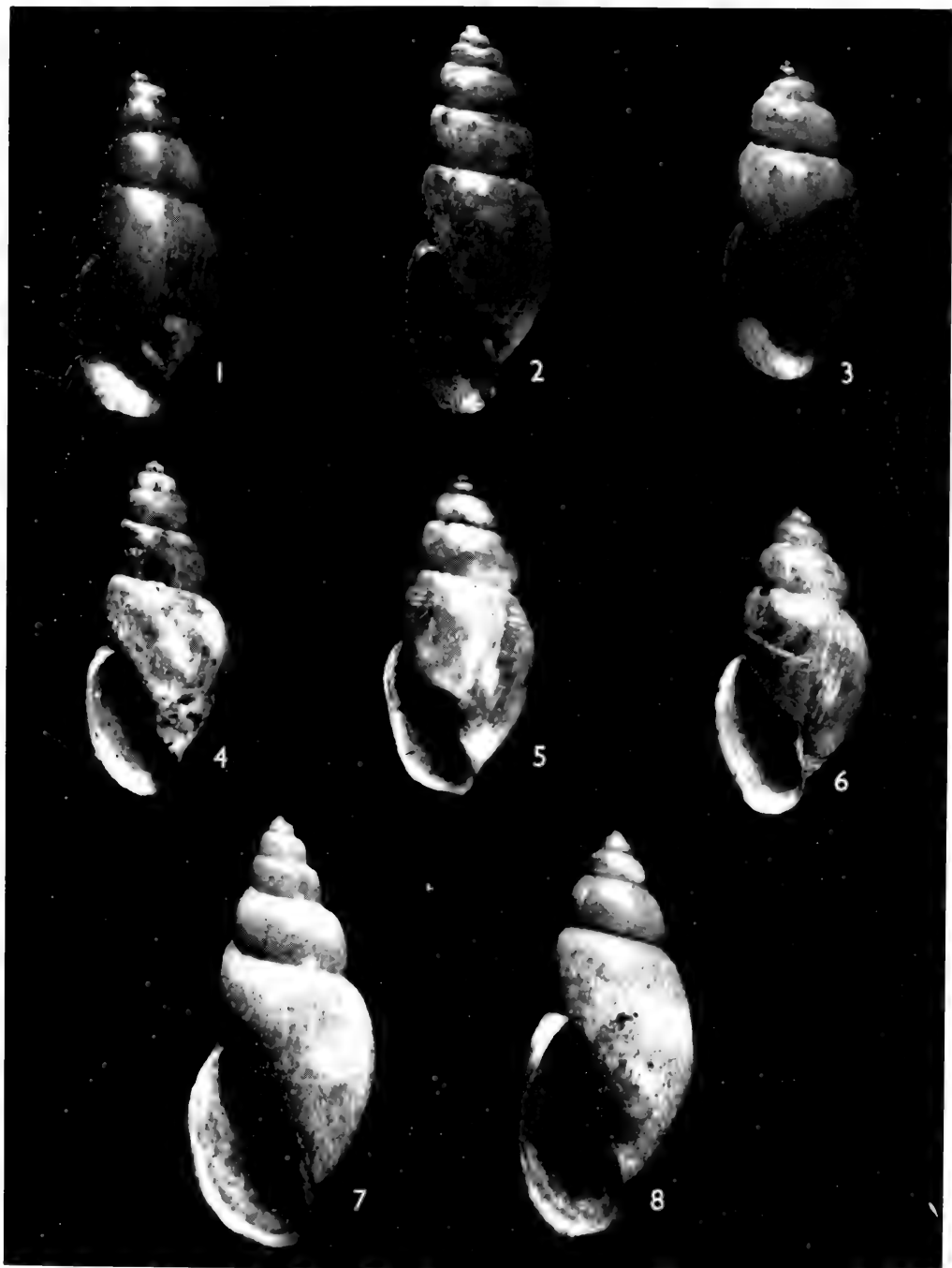


PLATE 10

Bulinus scalaris, apical whorls of one of the syntypes to show ribbing and carination. (× 50.)

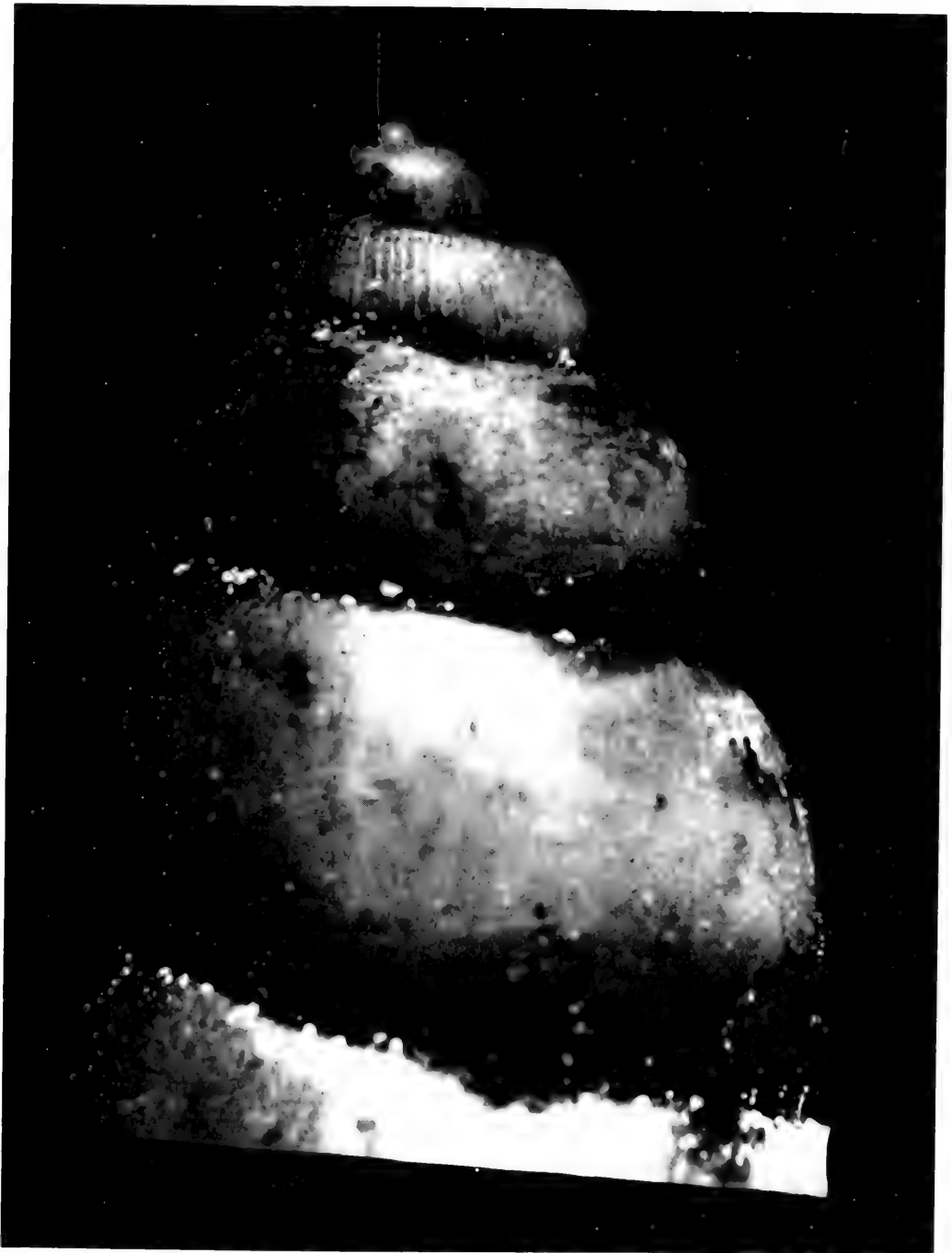


PLATE II

- FIGS. 1-3. *Bulinus crystallinus*, syntypes, B.M. (N.H.) coll. no. 93.2.4.636-8.
FIGS. 4-7. *B. crystallinus*, Salzar, Cuanza Norte.
FIGS. 8-11. *Bulinus truncatus rohlfsi*, Lagoa Cabemba, Luanda.
FIGS. 12-15. *B. truncatus rohlfsi*, Lagoa Panguila, Luanda.
FIGS. 16-19. *B. truncatus rohlfsi*, laboratory bred from stock originating from
Lagoa Cabemba.

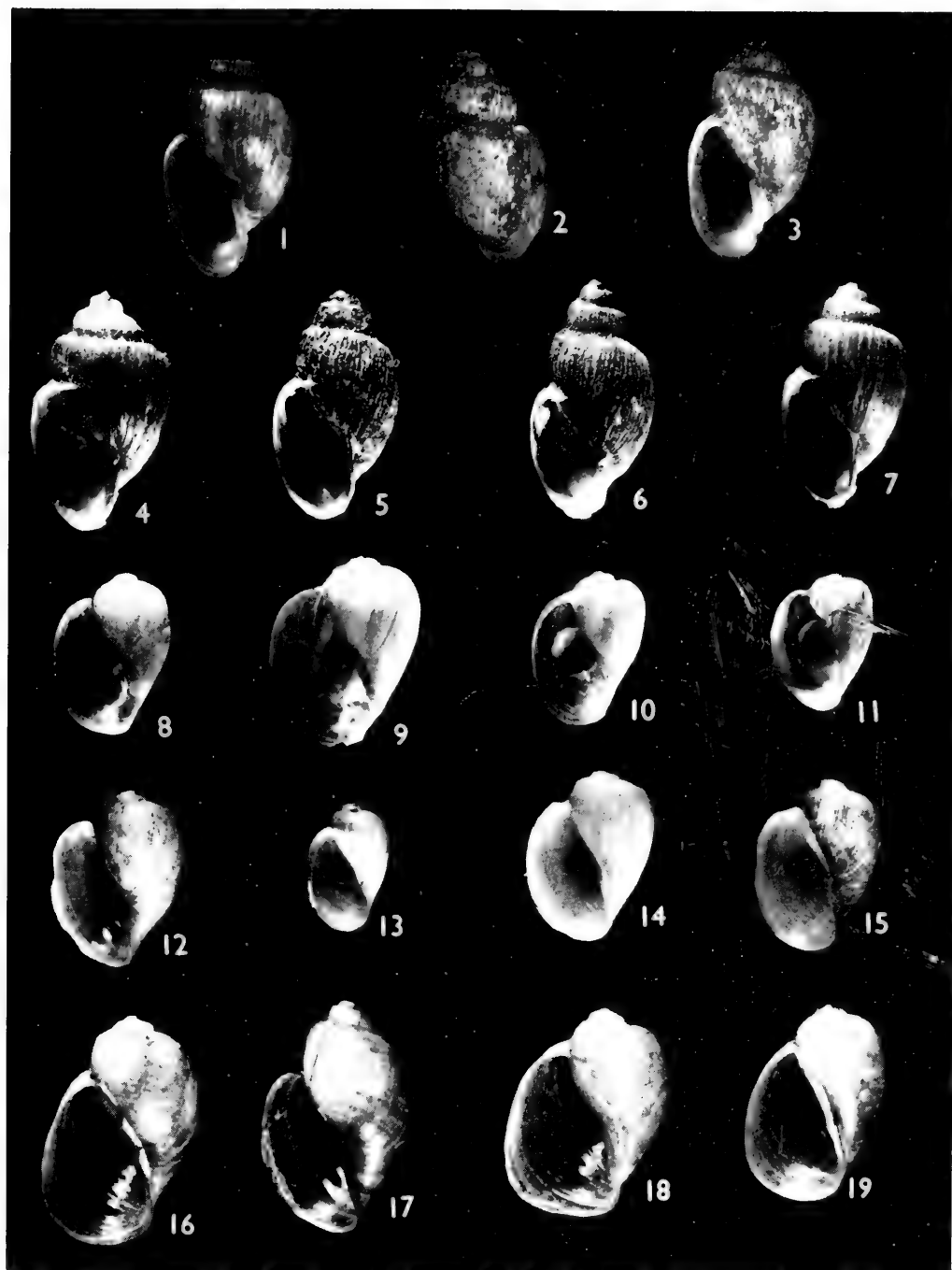


PLATE 12

Lymnaea natalensis.

- FIG. 1. *L. bocageana*, syntype, B.M. (N.H.) coll. no. 93.2.4.1341.
FIG. 2. *L. orophila*, syntype, B.M. (N.H.) coll. no. 93.2.4.1344.
FIG. 3. *L. sordulenta*, syntype, B.M. (N.H.) coll. no. 93.2.4.1332.
FIG. 4. *L. succinoides* (= *benguelensis*), syntype, B.M. (N.H.) coll. no. 76.6.8.55.



PLATE 13

Lymnaea natalensis.

- FIG. 1. *L. natalensis*, Quissol 1, Malange.
- FIG. 2. *L. natalensis*, Quissol 2, Malange.
- FIG. 3. *L. natalensis*, Lagoa Panguila, Luanda.
- FIG. 4. *L. natalensis*, Fazenda Tentativa, Luanda.
- FIG. 5. *L. natalensis*, Capemba & San Jose, Huila.
- FIG. 6. *L. natalensis*, Cangombe, Huila.



PLATE 14

- FIGS. 1-3. *Succinea badia*, syntypes, B.M. (N.H.) coll. no. 93.2.4.936-8. (\times 5).
FIGS. 4, 5. *S. concisa*, syntypes, B.M. (N.H.) coll. no. 93.2.4.950-1.
FIG. 6. *S. patentissima*, Lagoa Lumango, Luanda.
FIGS. 7, 8. *Bellamyia unicolor*, Rio Cuije, Malange. (\times 3).
FIG. 9. *Gabbia kisalensis*, Rio Cuije, Malange.

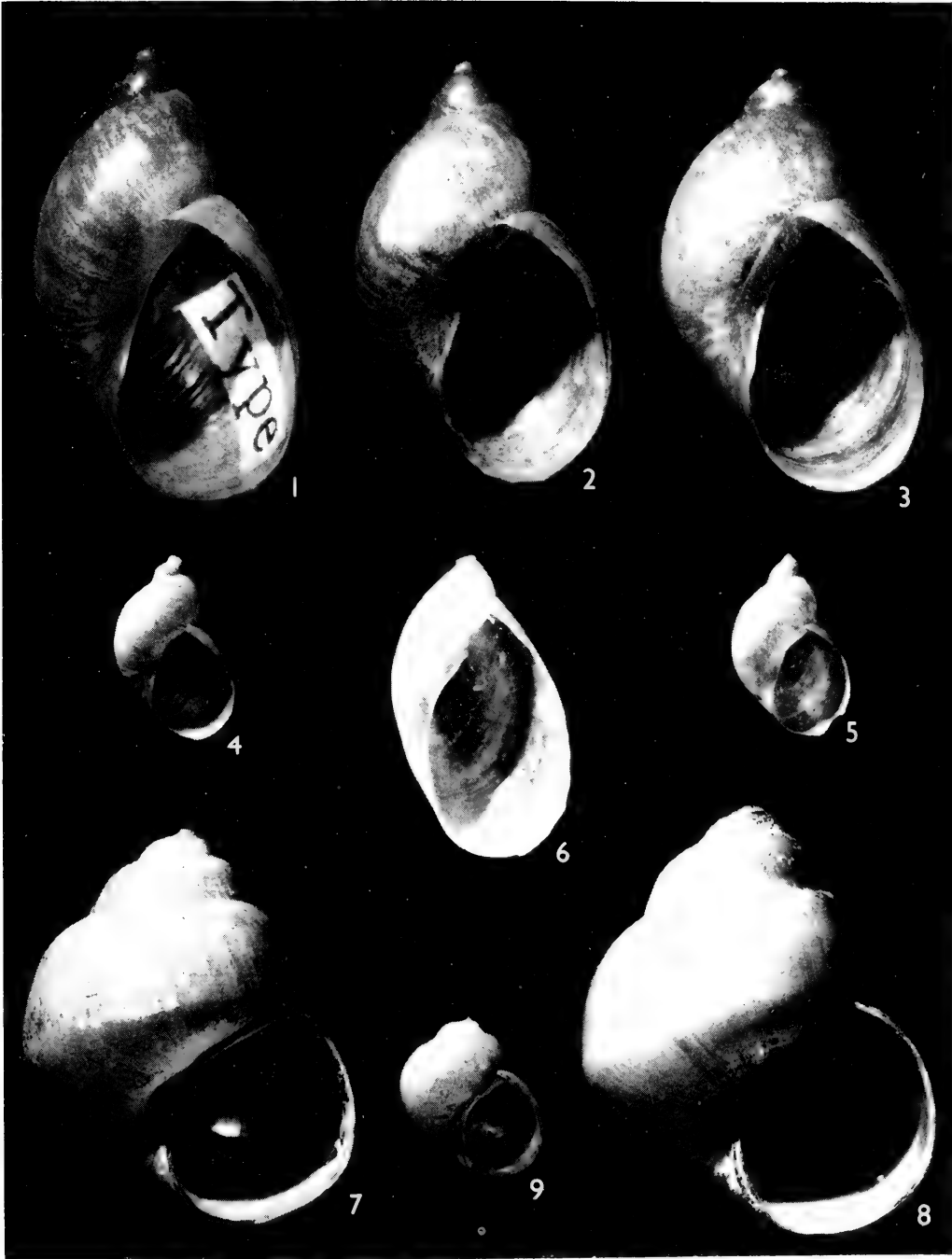


PLATE 15

FIG. 1. *Lanistes ovum*, specimen from the Welwitsch collection, B.M. (N.H.) coll. no. 93.2.4.1821. ($\times 1.25$).

FIG. 2. *L. ovum*, reputed paratype, B.M. (N.H.) coll. no. 196279. ($\times 1.25$).

FIG. 3. *L. libycus*, Rio Lucalla, Malange. ($\times 2$).

FIG. 4. *L. ovum*, Lagoa Matoz, Luanda. ($\times 1.75$).

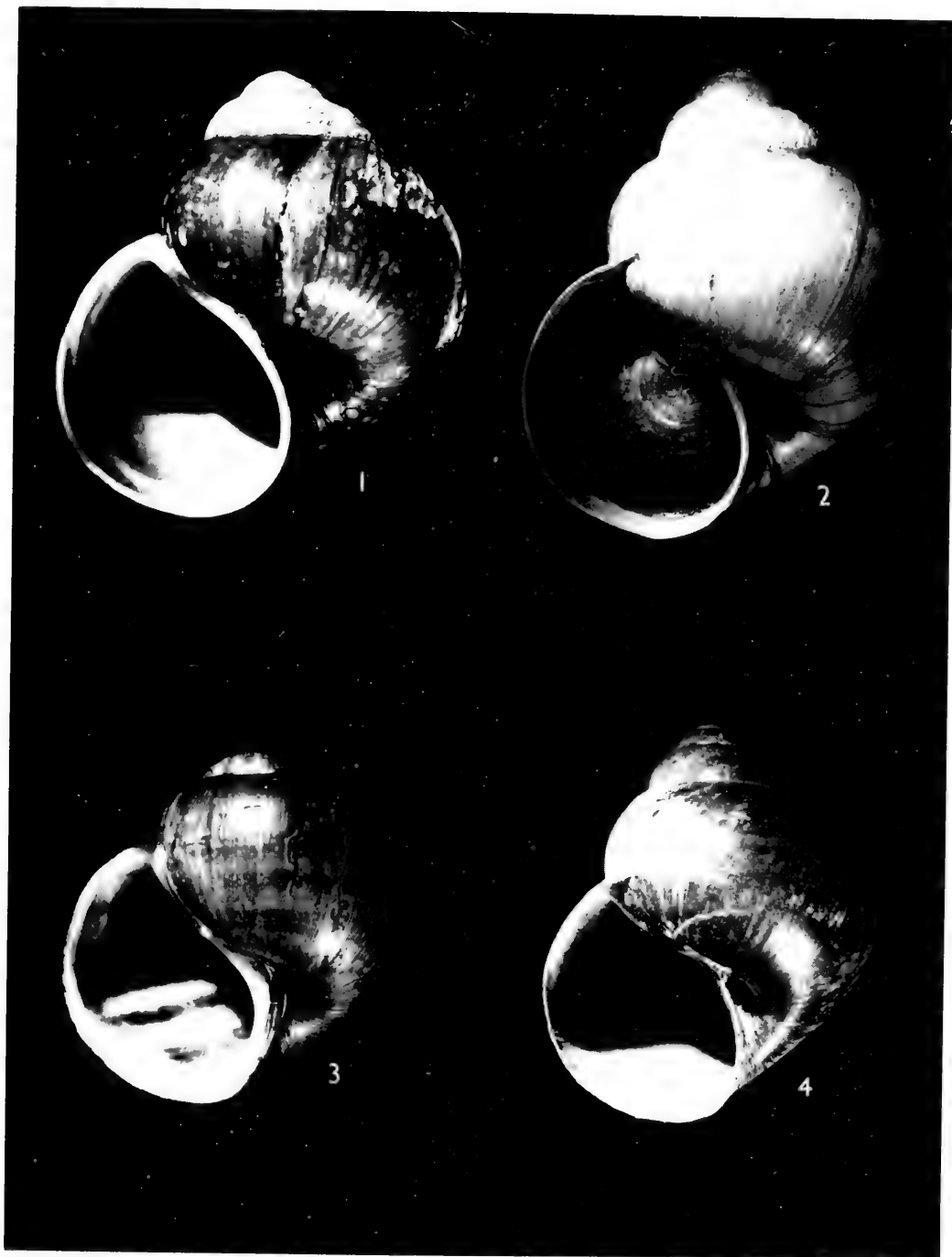
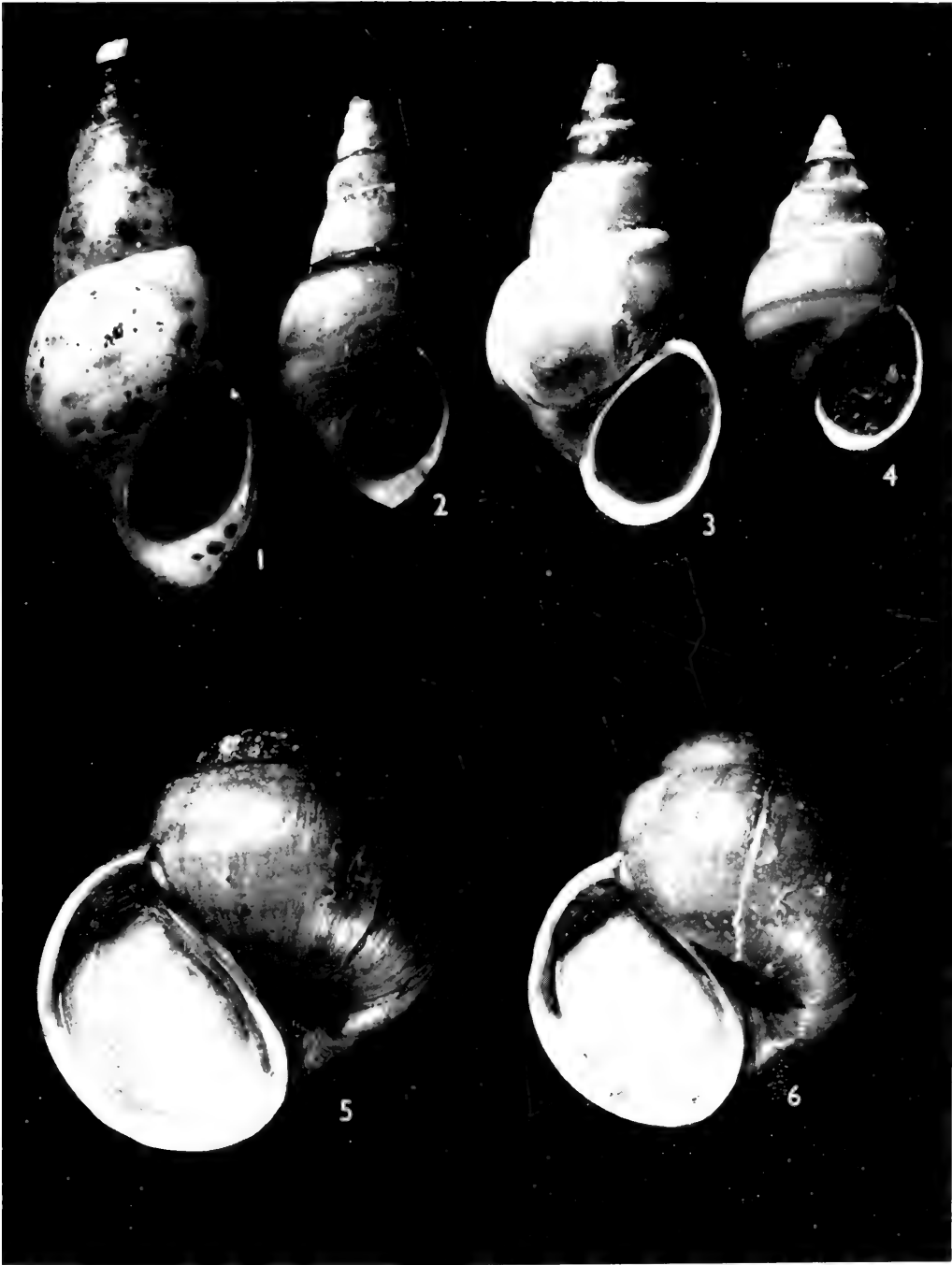


PLATE 16

- FIG 1. *Melanoides tuberculata*, Fazenda Tentativa, Luanda.
FIG. 2. *M. tuberculata*, Lagoa Quilunda, Luanda.
FIGS. 3, 4. *Cleopatra bulimoides*, Pungo Andongo, Cuanza Norte, B.M. (N.H.)
coll. no. 76.6.8.53.
FIGS. 5, 6. *Lanistes libycus*, syntypes, B.M. (N.H.) coll. no. 93.2.4.1814-5. ($\times 2$).





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FROM OFF THE COAST OF
SOUTH AFRICA



WILLIAM G. INGLIS

BULLETIN OF
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NEW MARINE NEMATODES FROM OFF THE COAST OF SOUTH AFRICA

By WILLIAM G. INGLIS

SYNOPSIS

Eight new species and two new genera of free-living marine nematodes are described from off the coast of South Africa, thus : Desmodoridae : *Desmodora cuddlesae* sp. nov.; *Bla nini* gen. et sp. nov.; *Sigmophora brevispiculata* sp. nov. Cyatholaimidae : *Choniolaimus wieseri* sp. nov.; *Longicyatholaimus dayi* sp. nov.; *Xyzzors fitzgeraldae* gen. et sp. nov. Comesomatidae : *Mesonchium janetae* sp. nov. Linhomoeidae : *Linhomoeus timmi* sp. nov. The form of the lateral differentiation in the genus *Mesonchium*, in particular, and the families Cyatholaimidae, Chromadoridae and Comesomatidae, in general, is discussed and it is concluded there is a fixed relationship between the total area of the differentiation and the area of the punctations which compose it. It is suggested that the punctations are canals which are associated with moulting.

THROUGH the courtesy of Professor J. H. Day of the University of Cape Town, Republic of South Africa I have been able to study some free-living marine nematodes collected by the Department of Oceanography of that University. The majority of the specimens are enoploids and will be the subject of a separate publication while the present report deals with the non-enoploid species only. All the specimens were picked by hand from material brought up by a trawl or grab and were fixed and preserved in formalin. Their condition is rather poor, the most obvious result being the apparent loss of body setae, but sufficiently good to warrant description.

The specimens were studied in glycerine after clearing by the slow method described elsewhere (Inglis, 1962).

There are eight new species, two of which are further referred to new genera, thus :

CHROMADORIDEA.

Desmodoridae.

Desmodora cuddlesae sp. nov. (p. 532).

Bla nini gen. et sp. nov. (p. 534).

Sigmophora brevispiculata sp. nov. (p. 537).

Cyatholaimidae.

Choniolaimus wieseri sp. nov. (p. 539).

Longicyatholaimus dayi sp. nov. (p. 542).

Xyzzors fitzgeraldae gen. et sp. nov. (p. 544).

Comesomatidae.

Mesonchium janetae sp. nov. (p. 547).

MONHYSTERIDEA.

Linhomoeidae.

Linhomoeus timmi sp. nov. (p. 550).

**CHROMADORIDEA
DESMODORIDAE**

***Desmodora cuddlesae* sp. nov.**

Material Studied

2 ♂♂. Coarse white sand at a depth of 27 metres. 32° 02' S./18° 17' E. on 2.7.61. (Department of Oceanography reference number: WCD 91). B.M. (N.H.) Reg. No. 1962. 605. (1 ♂ was destroyed accidentally).

Ratios			
<i>a</i>	<i>b</i>	<i>c</i>	Body Length (mm.)
34.5	7.0	13.5	1.76
38.8	8.6	14.1	1.98

Measurements (in mm. in order of body lengths above)

Body breadth : 0.051 ; 0.051. Oesophagus length : 0.25 ; 0.23. Oesophagus bulb length : 0.052 ; 0.050. Head diameter : 0.024 ; 0.024. Diameter of cephalic cap : 0.043 ; 0.039. Length of posterior cephalic setae : 0.004 ; 0.004. Length of body setae : 0.006 ; 0.007. Amphid, length/breadth : 0.038/0.037 ; 0.037/0.026. Distance of anterior edge of amphid from anterior end : 0.012 ; not measured as head very contracted. Tail length : 0.13 ; 0.14. Cloacal diameter : 0.049 ; 0.051. Spicule length : 0.042 ; 0.058. Length of gubernaculum : 0.012 ; 0.016.

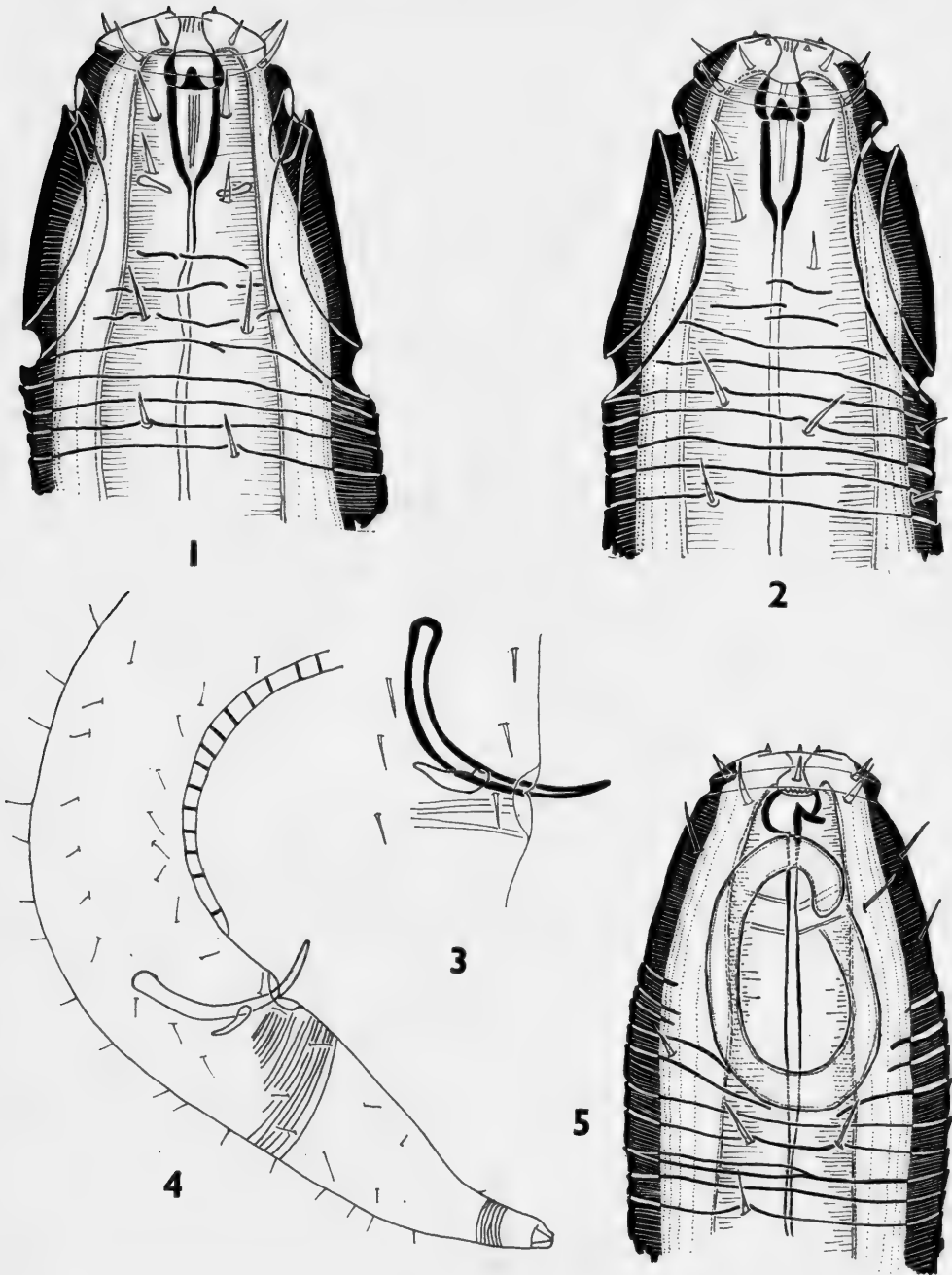
Cuticle

The cuticle is thick with the usual prominent striations so that it appears to be ringed. The anterior end of the body, the cephalic cap, is without striations to about the posterior ends of the amphids (Text-figs. 1, 2, 5). There are six files of longish setae running the whole length of the body. There are no couplings between the cuticular rings.

Head and Oesophagus

The head is characterized by very large ovoid amphids and a distinctly off-set lip region (seen in one specimen only as the head is retracted in the other). The lip region carries three circles of setae : an inner circle of six short, an intermediate circle of six longer and an outer circle of four much longer setae (Text-figs. 1, 2, 5). No *en face* view was prepared because of the small number of specimens but from a study of the head from all other aspects the mouth opening appears to be bounded by twelve rugae but this could be a misinterpretation of folded cuticle. The anterior end of the oesophagus is cupped ventrally for the reception of a large tooth-like structure developed from the dorsal sector of the oesophagus while the anterior edge of the oesophagus forms a slightly dentate ring. In lateral view there are what at first appear to be small teeth on the ventral side of the oesophageal cup but more detailed study suggests that this is a misinterpretation of the cupped anterior ends of the ventro-lateral sectors and that, in fact, no teeth are present. Confirmation of this must await the study of the head, or a similar head, in an *en face* preparation.

The oesophagus is typical with a short posterior bulb.



FIGS. 1-5. *Desmodora cuddlesae* sp. nov. Fig. 1. Dorsal view of head. Fig. 2. Ventral view of head. Fig. 3. Detail of spicules and gubernaculum. Fig. 4. Male tail. Fig. 5. Lateral view of head with the dorsal surface to the right.

Tail and Reproductive Apparatus

The tail is conoid and the terminal zone is without cuticular markings. Anterior to the cloacal opening is a long thickened ventral area in which there are 20 and 21 (in respective specimens) supplementary organs. I was unable to prepare a ventral view of the tail and am unable to add any other information on the structure of these organs. The spicules are round proximally and taper evenly to fine sharp points distally. The gubernaculum is relatively simple (Text-figs. 3, 4).

Discussion

This species is characterized by the very large amphids, the smooth cephalic cap, the non-cephalate spicules and the form of the pre-cloacal supplements.

Bla nini gen. et sp. nov.*Material Studied*

2 ♂♂, 2 ♀♀, 1 larva. Coarse white sand at a depth of 27 metres. 32° 02' S./18° 17' E. on 2.7.61. (Ref. No. WCD 91). B.M. (N.H.), Reg. Nos. 1962. 611-614.

	Ratios			V	Body Length (mm.)
	a	b	c		
Males	30.8	7.0	18.6		1.6
	39.1	8.6	19.4		1.8
Females	29.1	8.0	13.9	61.2	1.6
	32.7	7.4	15.5	58.8	1.7
Larva	32.6	7.8	12.3		1.4

Measurements (in mm. in order of body lengths above)

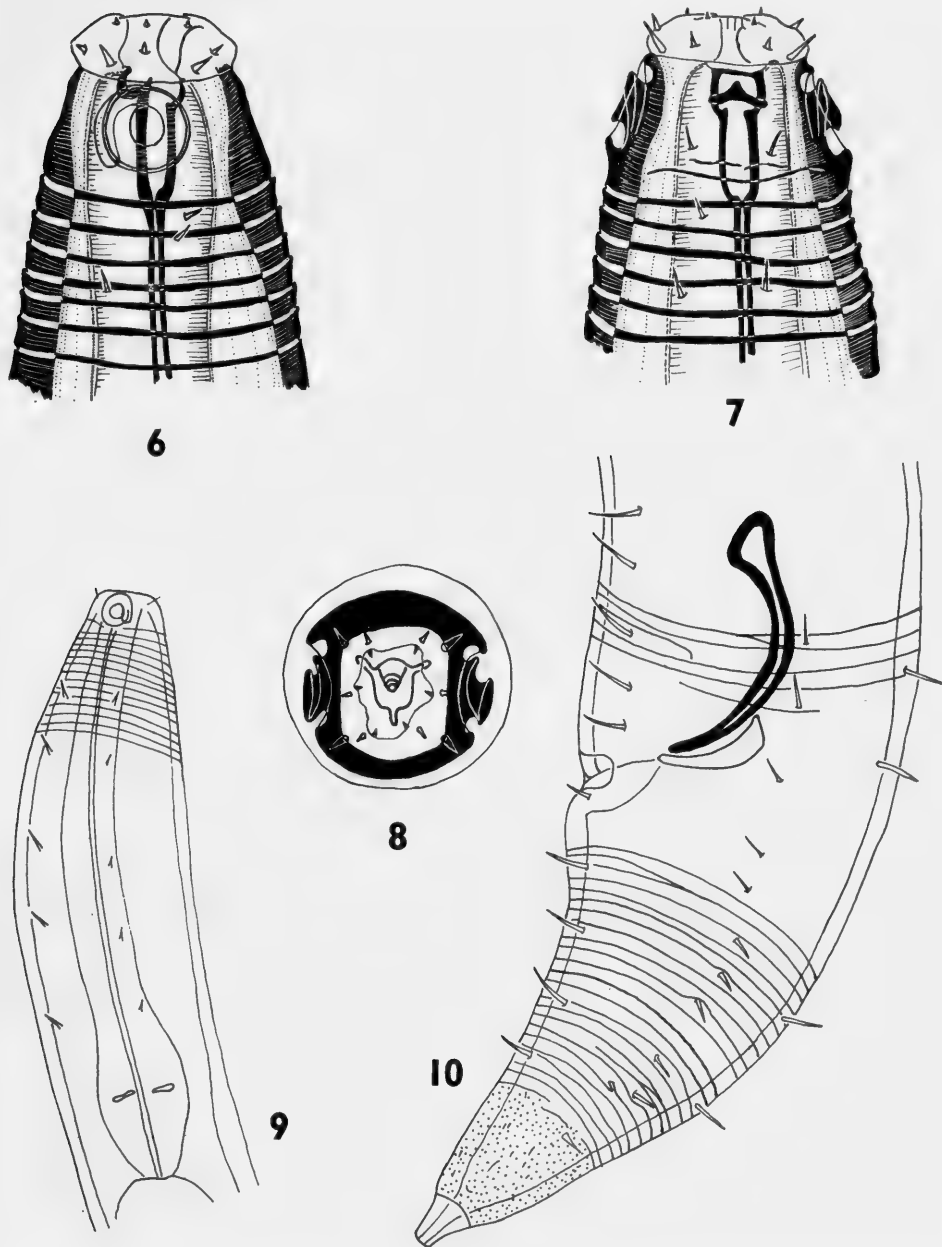
MALES. Body breadth : 0.052 ; 0.046. Oesophagus length : 0.23 ; 0.21. Head diameter : 0.024 ; 0.022. Length of cephalic setae, long/short : 0.006/0.003 ; 0.006/. . . Diameter of amphid : 0.013 ; 0.013. Tail length : 0.086 ; 0.093. Cloacal diameter : 0.049 ; 0.044. Length of dotted terminal portion of tail : 0.030 ; 0.031. Spicule length : 0.047 ; 0.047. Gubernaculum length : 0.018 ; 0.019.

FEMALES. Body breadth : 0.055 ; 0.054. Oesophagus length : 0.20 ; 0.23. Head diameter : 0.020 ; 0.023. Length of cephalic setae, long/short : 0.006/0.003 ; 0.006/0.002. Diameter of amphid : 0.013 ; 0.013. Distance of amphid from anterior end : 0.006 ; 0.007. Tail length : 0.115 ; 0.103. Anal diameter : 0.043 ; 0.046. Length of dotted terminal portion of tail : 0.054 ; 0.044. Distance of vulva from anterior end of body : 0.098 ; 1.00.

LARVA. Body breadth : 0.043. Oesophagus length : 0.18. Head diameter : 0.023. Length of cephalic setae, long/short : 0.007/not seen. Diameter of amphid : 0.010. Tail length : 0.114. Anal diameter : 0.042. Length of dotted terminal portion of tail : 0.034.

Cuticle

The cuticle is thick and has the usual ringed appearance. There are no couplings between the rings. The cuticle of the cephalic cap is without markings of any kind. There are six files of setae running the full length of the body.



FIGS. 6-10. *Bla nini* gen. et sp. nov. Fig. 6. Lateral view of head with dorsal surface to the left. Fig. 7. Dorsal view of head. Fig. 8. *En face* view of head. Fig. 9. Oesophagus. Fig. 10. Lateral view of male tail.

Head and Oesophagus

The head bears three circles of setose sense organs, six very short setae in an inner circle, six longer in an intermediate circle and four relatively very long in an outer circle. These setae are all located on an off-set anterior portion of the head, as in the previous species (Text-figs. 6, 7). The large circular and spiral amphids lie immediately posterior to this off-set portion. In all the specimens, except that figured, the head is retracted so that it has not been possible to establish the form of the mouth opening in *en face* view but it has been possible to establish the shape of the buccal cavity and the distribution of the cephalic sense organs (Text-fig. 8). The cavity at the anterior end of the oesophagus into which the prominent dorsal "tooth" projects (Text-fig. 6) is roughly rectangular in shape while the very thick cuticle of the anterior part of the head is also rectangular in cross section. Whether this shows the shape of the part of the buccal cavity anterior to the end of the oesophagus or not is uncertain since there may be tissue lining this space which I have been unable to see. I have been unable to see a dentate ring at the anterior end of the oesophagus, as in *Desmodora cuddlesae*, and the structures usually described as ventral teeth appear to be the anterior edges of the ventro-lateral sectors of the oesophagus seen in optical section.

The oesophagus is expanded posteriorly to form a small bulb with, apparently, one small plasmatic interruption (Text-fig. 9). The oesophagus of *D. cuddlesae* looks exactly the same as this.

Tail

The tail is short and stout in both sexes with the terminal zone marked by circular punctations, or rod elements (Text-fig. 10).

Male

The male tail bears two files of long, stout setae on its ventral surface. The spicules are slightly cephalate proximally and end distally in very sharp points. The gubernaculum is small and lies close to the spicules. There are no pre-cloacal supplements of any kind (Text-fig. 10).

Discussion

The form of the terminal zone of the tail restricts the allocation of this species to one of two genera: *Croconema* Cobb, 1920 or *Xenodesmodora* Wieser, 1951. The first of these genera is characterized by a most unusual and irregular arrangement of the cephalic sense organs (see Schuurmans Stekhoven, 1950; Wieser, 1951) which are distributed in irregular rows on the cephalic cap. Even in *Croconema mammallatum* Steiner and Hoeppli, 1926, where the arrangement of the cephalic setae is least irregular, they are still not arranged in the regular and typical way found in the present species. The second of these genera is characterised by cephalic sense organs arranged in the more typical way, that is in transverse circles, but the type species, *X. porifera* Wieser, 1951, is known on the basis of one female only. Further, the description appears in one of Wieser's earlier publications and is not up to his usual standard so that although the genus is claimed to be further characterized by very small pharyngeal teeth their structure cannot be established

on the basis of Wieser's description or his figures. The dorsal "tooth" in the present specimens is large and prominent and I prefer to refer them to a new genus, at least until a thorough study can be made of specimens referable to *Xenodesmodora* obtained from or near the type locality.

The genus *Bla* may be diagnosed thus :

Desmodoridae : Desmodorinae (sensu Chitwood, 1936) : amphid large, almost circular in shape ; cephalic sense organs setose, arranged in three circles ; dorsal tooth-like structure of oesophagus large ; posterior part of tail with punctations.

Type Species : *Bla nini* sp. nov.

Sigmophora brevispiculata sp. nov.

Material Studied

1 ♂, 2 ♀. Khaki mud at a depth of 54 metres. 32° 05' S./18° 16' E. on 2.7.61. (Ref. No. WCD 94). B.M. (N.H.) Reg. Nos. 1962. 608-610.

	Ratios				
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	Body Length (mm.)
Male	22.2	5.1	15.8		1.8
Females	24.2	7.4	19.6	55.9	2.9
	33.3	7.2	22.6	55.6	3.3

Measurements (in mm. in order of body lengths)

MALE. Body breadth : 0.081. Oesophagus length : 0.351. Head diameter : 0.067. Diameter of amphid : 0.018. Tail length : 0.114. Cloacal diameter : 0.090. Spicule length : 0.117. Gubernaculum length : 0.054.

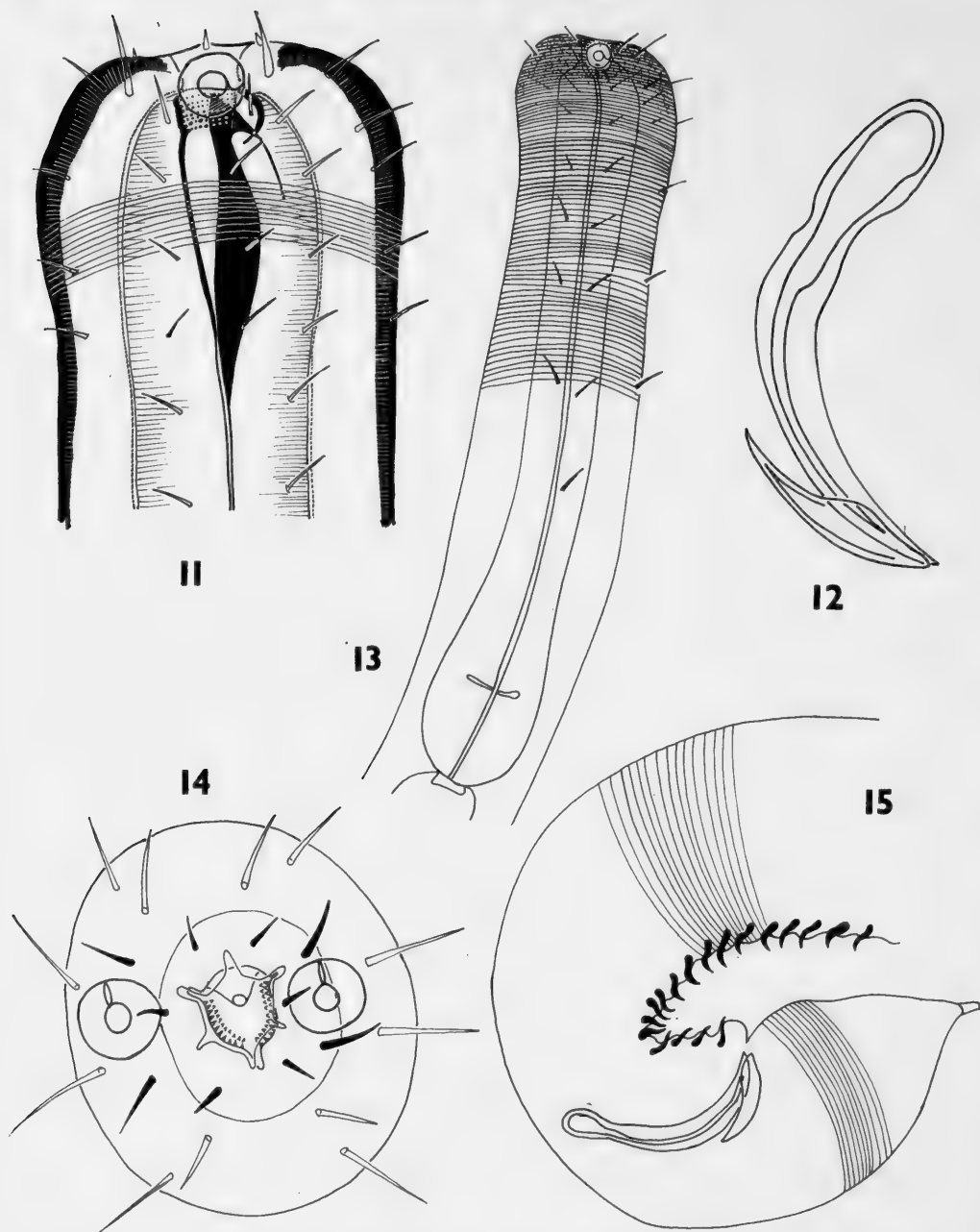
FEMALES. Body breadth : 0.12 ; 0.099. Oesophagus length : 0.390 ; 0.456. Head diameter : 0.063 ; 0.074. Diameter of amphid : 0.017 ; 0.019. Length of cephalic setae : 0.019 ; 0.019. Length of cervical setae : 0.017 ; 0.017. Tail length : 0.148 ; 0.146. Anal diameter : 0.075 ; 0.084. Distance of vulva from anterior end of body : 1.62 ; 1.83. Size of eggs : 0.11 × 0.28.

Cuticle

The cuticle is fairly thick and is marked by rather fine striations which continue to the extreme anterior end of the body. There are granulations in the cuticle at the anterior end of the body (Text-fig. 13).

Head and Oesophagus

The head is blunt and there is no cephalic helmet. In all the specimens the head is contracted so that the amphids probably appear to lie much further forward than is really the case in life. The amphids are circular and spiral (Text-fig. 11). The mouth opening appears to be bounded by six lip-lobes (Text-fig. 14) but the retracted condition of the head makes this difficult to establish. The mouth appears to be surrounded by an intermediate circle of six short setae and an outer circle of four much longer setae (Text-fig. 14) but the position is complicated by the presence of rows of somewhat similar setae on the cervical region of the body. The presence of an inner circle of sense organs cannot be established because of the contracted head. A large, prominent tooth-like structure is developed from the



FIGS. 11-15. *Sigmophora brevispiculata* sp. nov. Fig. 11. Lateral view of head with dorsal surface to the right. Note the S-shaped dorsal tooth. Fig. 12. Detail of spicules and gubernaculum. Fig. 13. Oesophagus. Fig. 14. *En face* view of head. The setae which are interpreted as composing the cephalic sense organs are solid black. Fig. 15. Lateral view of male tail.

dorsal sector of the oesophagus while the ventro-lateral sectors are cupped with seven rows of denticles on the walls (Text-figs. 11, 14).

The oesophagus is fairly massive with a slight swelling posteriorly but there is no massive bulb nor is there any thickening of the lining of the oesophagus posteriorly (Text-fig. 13).

Male

The tail is very short and stout (in both sexes—Text-fig. 15) and there are thirty-nine cuticular crochet shaped supplements anterior to the cloacal opening. These structures are arranged in one median ventral row and each is triple-ended i.e. the distal, projecting end divides into three parts. The gubernaculum is very simple and the spicules are swollen and rounded proximally. They narrow more distally and then taper evenly to a fine point (Text-fig. 12).

Discussion

The presence of the crochet shaped pre-cloacal supplements on the male tail restricts the placements of this species to one of two genera, *Sigmophora* Cobb, 1933 or *Onyx* Cobb, 1891. It differs from the species referred to both in the form of the posterior end of the oesophagus, although this may be due to poor fixation and I do not lay too much stress on it. It further differs from the species referred to *Onyx* in the shape of the dorsal tooth, the shape of the pre-cloacal supplements and in the presence of denticles on the ventro-lateral sectors of the buccal cavity. Conversely it resembles the species referred to *Sigmophora* in all three characters, but differs from them in the very short spicules which are in general shape very similar to those illustrated by Filipjev (1918) for *Onyx perfectus* Cobb, 1891, and a little less similar to those shown by Wieser (1954) for *O. septempapillatum* Wieser, 1954. Whether these two genera should continue to be treated as distinct is doubtful, certainly the species referred to *Onyx* form a heterogeneous group. On the other hand the species referred to *Sigmophora* form a much more uniform group from which the present species differs only in the very short spicules. I therefore prefer to refer the South African specimens to the genus *Sigmophora* until further information is available on the two genera *Onyx* and *Sigmophora*.

CYATHOLAIMIDAE

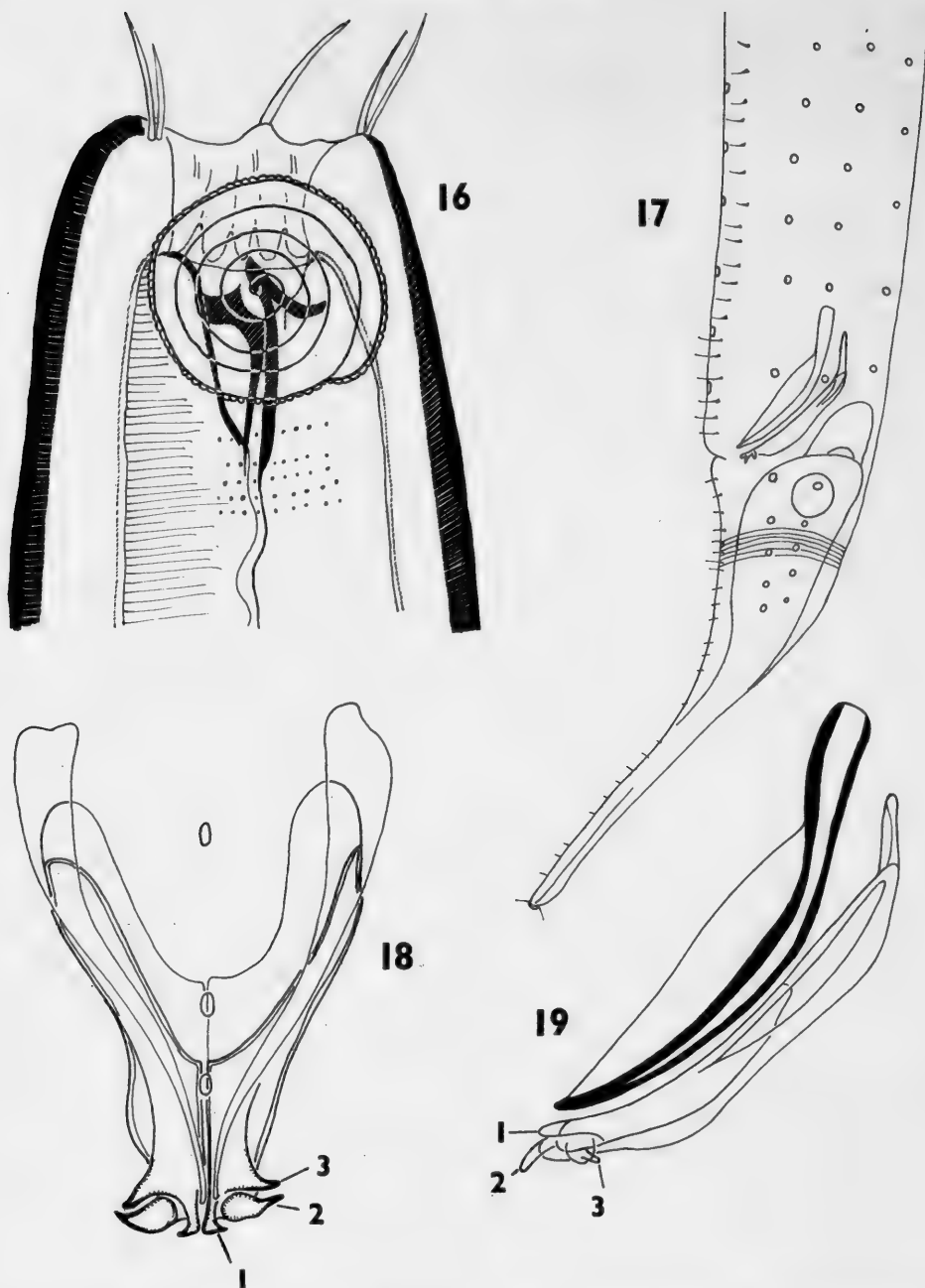
Choniolaimus wieseri sp. nov.

Material Studied

1 ♂, 1 ♀. Coarse white sand at a depth of 39 metres. 32° 05' S./18° 17' E. on 2.7.61 (Ref. No. WCD 93). B.M. (N.H.) Reg. No. 1962. 606/7.

	Ratios				Body Length (mm.)
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	
Male	34.8	7.0	10.3		3.2
Female	28.3	5.8	8.8	53.2	2.6

MALE. Body breadth : 0.092. Oesophagus length : 0.46. Head diameter : 0.048. Length of cephalic setae, long/short : 0.018/0.016. Diameter of amphid : 0.030. Tail length : 0.31. Cloacal diameter : 0.084. Spicule length : 0.096. Gubernaculum length : 0.093.



FIGS. 16-19. *Choniolaimus wieseri* sp. nov. Fig. 16. Lateral view of head with dorsal surface to the right. Fig. 17. Lateral view of male tail. Fig. 18. Ventral view of spicules and gubernaculum. Fig. 19. Lateral view of spicules and gubernaculum (The numbers indicate corresponding structures).

FEMALE. Body breadth : 0.093. Oesophagus length : 0.45. Head diameter : 0.043. Length of cephalic setae, long/short : 0.018/0.015. Diameter of amphid : 0.024. Tail length : 0.30. Anal diameter : 0.084. Distance of vulva from anterior end of body : 1.40.

Cuticle

The cuticle is marked by transverse rows of small punctations and the lateral markings are slightly larger and further apart than those on the rest of the body. There are eight files of Type-1 campaniform organs running the full length of the body and there is a lateral file of seven Type-2 organs on each side of the body running posteriorly from the amphids with a similar set of five running posteriorly from the cloacal or anal openings. These campaniform organs are very similar in structure to the organs of the same name in the insects and the Type-1 is elliptical in shape with a sheet of cuticle projecting into it while the Type-2 is circular with a central boss (see Inglis, 1963).

Head and Oesophagus

The head is retracted in both specimens so that the amphid appears to lie far anteriorly and the cephalic setae appear to arise from the edge of the mouth opening (Text-fig. 16). The mouth is bounded by the usual twelve rugae ; there is a large dorsal cuticularized tooth-like structure and two smaller ventro-lateral tooth-like structures which are in fact two cuticular ridges seen in optical section—exactly as in *Longicyatholaimus dayi* (see p. 543). The amphid is large with five and a quarter spirals in both sexes. There is no oesophageal bulb or posterior expansion.

Male

The tail narrows rather suddenly posteriorly and anterior to the cloacal opening are ten small cup-like supplementary organs arranged in a file on the ventral surface of the body. These organs appear to be similar in structure to Type-2 campaniform organs but I cannot be sure on this point. In addition there are two files of stout ventro-lateral setae anterior to the cloacal opening. The spicules are simple with broad alae (Text-fig. 19). The gubernaculum is complex, almost as long as the spicules, with a dentate distal end. From the lateral aspect it appears slim and lightly built with a thin tail-like portion attached to its proximal end (Text-fig. 19) and with three small tooth-like structures developed from its distal end. In ventral view (Text-fig. 18) the massive structure of the gubernaculum is more easily appreciated and the tail-like proximal portion is seen to be extensive although rather delicate. The distal end has a pair of small tooth-like structures medially with two pairs of much larger structures flanking them. The corresponding parts are marked on Text-figs. 18 and 19.

Discussion

This species is certainly congeneric with *Choniolaimus macrodentatus* Wieser, 1959 and differs from it, apparently, in the structure of the gubernaculum, the number of pre-cloacal supplements, the shorter tail and the much longer cephalic setae. However, whether both species are congeneric with *C. papillatus* Ditlevsen, 1919 I am not sure. Thus Ditlevsen (1919) describes, and figures, a very distinct

post-oesophageal bulb and states "... there is no tooth in *Choniolaimus*". The dorsal tooth-like structure is very prominent in both *C. macrodentatus* and *C. wieseri* and there is certainly no oesophageal bulb in the latter species. Wieser does not comment on this point in describing *C. macrodentatus*. In spite of this I prefer to accept Wieser's interpretation of the genus and refer this new species to *Choniolaimus*, at least provisionally.

***Longicyatholaimus dayi* sp. nov.**

Material Studied

1 ♂, 1 larva. Khaki mud at a depth of 54 metres. 32° 05' S./18° 16' E. on 2.7.61. (Ref. No. WCD 94). B.M. (N.H.), Reg. Nos. 1962. 601/2.

	Ratios			Body Length (mm.)
	<i>a</i>	<i>b</i>	<i>c</i>	
Male	31.0	4.8	12.4	3.1
Larva	26.0	4.7	10.8	2.6

Measurements (in mm. male first)

Body breadth : 0.10 ; 0.10. Oesophagus length : 0.64 ; 0.55. Head diameter : 0.052 ; 0.043. Length of anterior cephalic setae : 0.008 ; 0.008. Length of posterior cephalic setae, long/short : 0.017/0.013 ; 0.018/0.013. Diameter of amphid : 0.014 ; 0.013. Distance of amphid from anterior end : 0.014 ; 0.011. Distance of excretory pore from anterior end of body : 0.21 ; 0.19. Tail length : 0.25 ; 0.24. Cloacal diameter : 0.082 ; 0.078. Spicule length : 0.065. Gubernaculum length : 0.038.

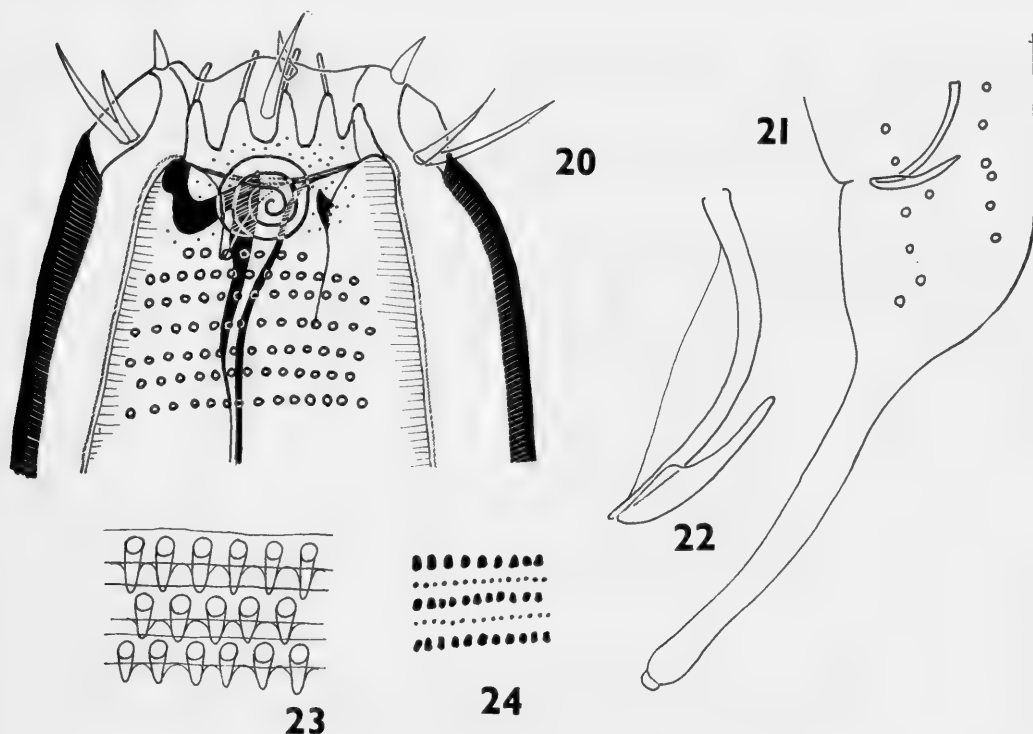
Cuticle

There is no lateral differentiation but the cuticular markings on the anterior end of the body from about the mid-point of the length of the oesophagus anteriorly are more prominent and different in shape from those more posteriorly. The more posterior markings take the form of alternate rows of large and small punctations which extend over the entire surface of the body (Text-fig. 24). The anterior markings are more complex and appear to move when studied under high magnification in a way comparable to the markings of the cuticle of *Euchromadora* species. The most obvious feature of the anterior cuticular marking is a series of transverse rows of large punctations (Text-fig. 20) which represent rods of dense material seen end on lying in the general mass of the cuticle at right angles to the plane of the external surface. These rods arise from an inner transverse ring of dense cuticular material lying in the inner part of the cuticle and end externally in a similar ring of dense material which is wedge-shaped in longitudinal section so that it is thin along its anterior edge and stout along its posterior edge. Thus the cuticle at the anterior end of the body is composed of a series of double rings of dense material, one external and one internal, connected by a series of rods of similar material. The external rings are so arranged that each lies partly over the ring immediately anterior to it and partly under the ring immediately posterior to it. The anterior edge of each external ring is uninterrupted while the posterior edge takes the form of a series of battlement-like processes which, as the rods of each

ring alternate with those of the rings immediately anterior and posterior to it, pass between the rods of the immediately posterior ring (Text-fig. 23). The structure of the cuticle in this species will be described and considered in much greater detail elsewhere. There are two lateral files of Type-1 campaniform organs (Inglis, 1963) on each side of the body which run the full length of the body. In one female specimen (which was not available to me before) I have found files of five Type-2 organs running posteriorly from the amphids just as in *Choniolaimus wieseri*.

Head and Oesophagus

The head is typically cyatholaimid with a mouth opening bounded by twelve rugae, an inner circle of six setose sense-organs and an outer circle of ten setae of which four are shorter than the other six. The amphid is spiral, with three and three quarter spirals in each specimen, and rather small (Text-fig. 20). The anterior end of the dorsal sector of the oesophagus is strongly cuticularized to form the usual tooth-like structure but the ventro-lateral sectors do not appear to be modified in a comparable way i.e. in accordance with the usual form of description, there are



FIGS. 20-24. *Longicyatholaimus dayi* sp. nov. Fig. 20. Lateral view of head with the dorsal surface to the left. Fig. 21. Lateral view of male tail. Fig. 22. Detail of spicules and gubernaculum. Fig. 23. Detail of cuticular structure on anterior end of body. Fig. 24. Detail of cuticular structure over major part of body (Figs. 23 and 24 are semi-diagrammatic).

no ventral teeth. The small tooth-like structure figured (Text-fig. 20) ventrally appears to arise from the edge of the ventral arm of the oesophageal lumen and appears to be unpaired. There is no posterior oesophageal swelling.

Male

The tail narrows rather suddenly about one third of its length posterior to the cloacal opening and terminates in a rather long flagellate portion. The spicules are lightly cuticularized and simple in structure with wide alae. The gubernaculum is simple and is wider proximally than it is distally (Text-fig. 22). There are no pre-cloacal supplements.

Discussion

This species differs from all others referred to the genus *Longicyatholaimus* in the simplicity of the gubernaculum, the form and length of the tail, in lacking lateral differentiation and, possibly, in the structure of the cuticular markings on the anterior end of the body. The possibility that it may warrant recognition as the type species of a new genus has been considered but in view of the rather poor condition of the specimens and the poverty of some of the descriptions available for related species I have preferred not to take this step.

Xyzzors fitzgeraldae gen. et sp. nov.

Material Studied

1 ♂. Khaki mud at a depth of 54 metres. 32° 05' S./18° 16' E. on 2.7.61. (Ref. No. WCD 94). B.M. (N.H.), Reg. No. 1962. 604.

Ratios			Body Length (mm.)
a	b	c	
45.6	6.8	15.3	3.6

Measurements (in mm.)

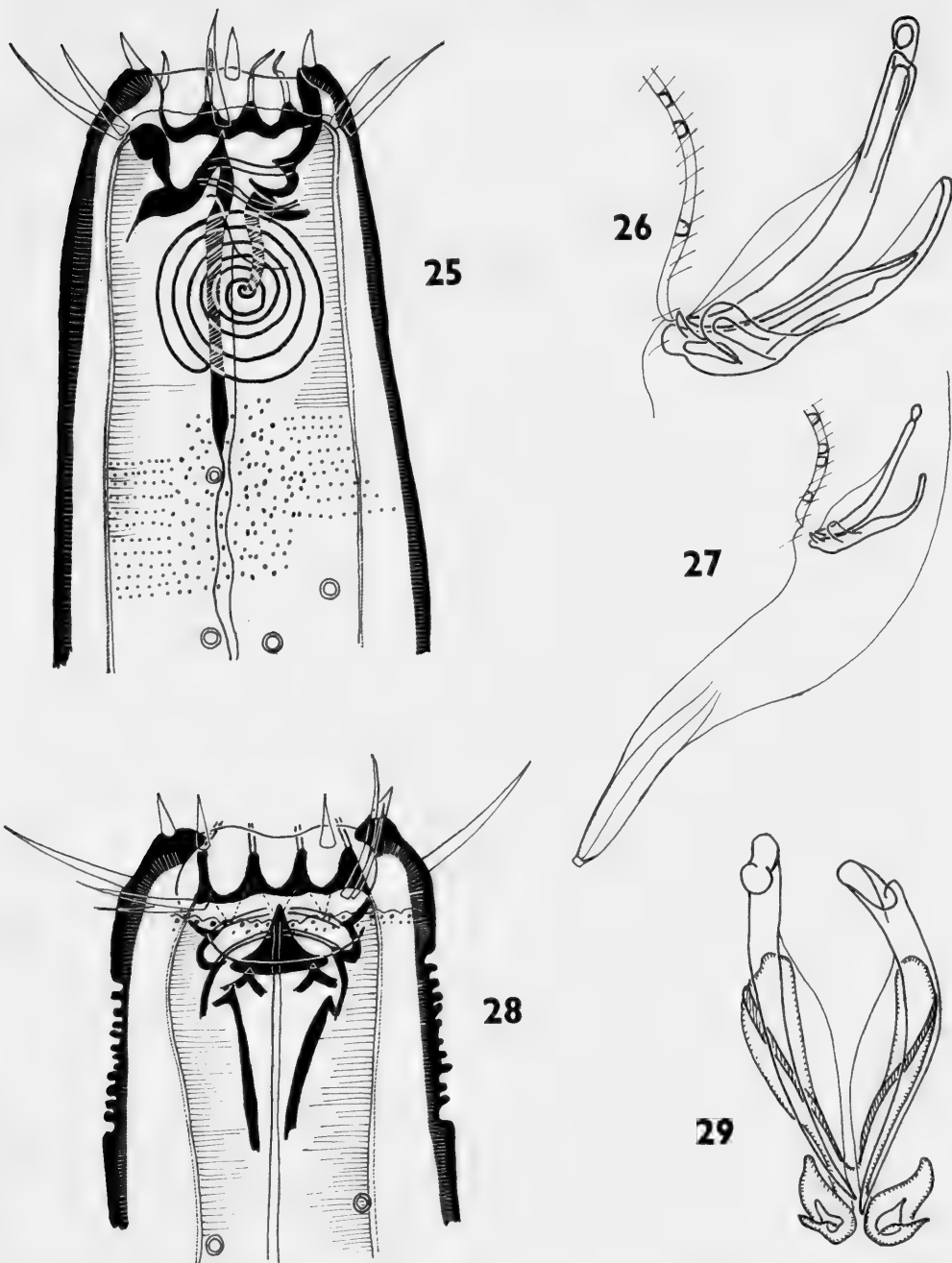
Body breadth : 0.079. Oesophagus length : 0.53. Head diameter : 0.048. Length of anterior cephalic setae : 0.005. Length of posterior setae, long/short : 0.020/0.018. Diameter of amphid : 0.023. Distance of amphid from anterior end of body : 0.018. Tail length : 0.236. Cloacal diameter : 0.077. Spicule length : 0.089. Gubernaculum length : 0.078.

Cuticle

The cuticle is marked by transverse rows of fine punctations which are replaced laterally by larger, irregularly arranged punctations along the whole length of the body. There are eight files of Type-1 campaniform organs running the full length of the body.

Head and Oesophagus

The head is blunt and bears six short setae in an inner circle and ten in an outer made up of six long and four short. The cuticular punctations start just posterior to the outer circle of setae. The amphids are large and multi-spiral with six and three-quarter spirals (Text-fig. 25). They are situated fairly far posterior to the anterior end of the body. The mouth opening is bounded by twelve rugae and the



FIGS. 25-29. *Xyzzors fitzgeraldae* gen. et sp. nov. Fig. 25. Lateral view of head with the dorsal surface to the left. Fig. 26. Detail of spicules and gubernaculum from the side. Fig. 27. Lateral view of male tail. Fig. 28. Dorsal view of head. Fig. 29. Ventral view of gubernaculum and spicules.

anterior end of the oesophagus is highly modified with a large dorsal tooth-like structure and what appear to be two pairs of smaller ventro-lateral teeth. These latter structures are in fact two cuticular ridges running round the cavity at the anterior end of each ventro-lateral sector of the oesophagus seen in section. In addition to this the anterior ends of the ventro-lateral sectors appear to be slightly modified and covered with thickened cuticle (Text-figs. 25, 28). The oesophagus is simple without a posterior swelling.

Tail and Reproductive Apparatus

The tail is fairly slim and tapers to a fairly narrow terminal part. The spinnerette is not off-set, although this may be due to the condition of the specimen. There are six small cup-like pre-cloacal supplements which are rather indistinct (Text-fig. 27).

The spicules are much more elaborate than is usual in species of the Cyatholaimidae. They are broadly alate along their distal two thirds and in lateral view appear to be double proximally—that is they appear to divide into two distinct shafts (Text-fig. 26). In a ventral view, however, this division is not complete and is due to the broad proximal ends being grooved along their dorsal and ventral surfaces (Text-fig. 29). The gubernaculum is slim proximally but becomes much stouter and elaborate distally where there are two lateral processes on each side. One, the more proximal is large and rounded while the more distal is smaller and more sharply tipped (Text-figs. 26, 29). There are two files of long ventro-lateral setae on the surface of the body anterior to the cloacal opening.

Discussion

This species is most similar to those referred by Wieser (1954, 1959) to his genus *Biarmifer* but differs most markedly in the structure of the spicules and in the distinct, irregular lateral differentiation. Wieser describes the characteristic form of the spicules in the species he refers to *Biarmifer* as having “ . . . two lists which are fused proximally and distally but separated medially by a lacuna ”. The condition in the present specimen is very different from this and appears to be unique among the species referred to genera of the family Cyatholaimidae with the possible exception of *Nannolaimus complicatus* Gerlach, 1957 where the figure suggests a comparable division of the proximal end of the spicule. The form of the gubernaculum is similar to that in *Biarmifer gibber* Wieser, 1959 but is more complicated. In the structure of the buccal cavity the present species appears to be most similar to *Pomponema* Cobb, 1917 but differs from the species referred to that genus in the irregular lateral differentiation, the form of the spicules and the form of the pre-cloacal supplements.

I, therefore, propose to refer this species to a new genus, *Xyzzors*, which may be diagnosed thus :

Cyatholaimidae : Cyatholaiminae : lateral differentiation irregular running full length of body ; buccal cavity with a very large dorsal tooth-like structure ; spicules complex with doubled proximal ends ; gubernaculum complex distally with only two processes.

Type species : *Xyzzors fitzgeraldae* sp. nov.

COMESOMATIDAE

Mesonchium janetae sp. nov.*Material Studied*

2 ♂♂, 1 ♀. Khaki mud at a depth of 54 metres. 32° 05' S./18° 16' E. on 2.7.61. (Ref. No. WCD 94). B.M. (N.H.), Reg. Nos. 1962. 599/600.

	Ratios				
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	Body Length (mm.)
Males	30.0	10.2	17.1		4.8
	37.3	11.4	15.6		5.6
Female	27.8	10.2	16.1	48.0	5.0

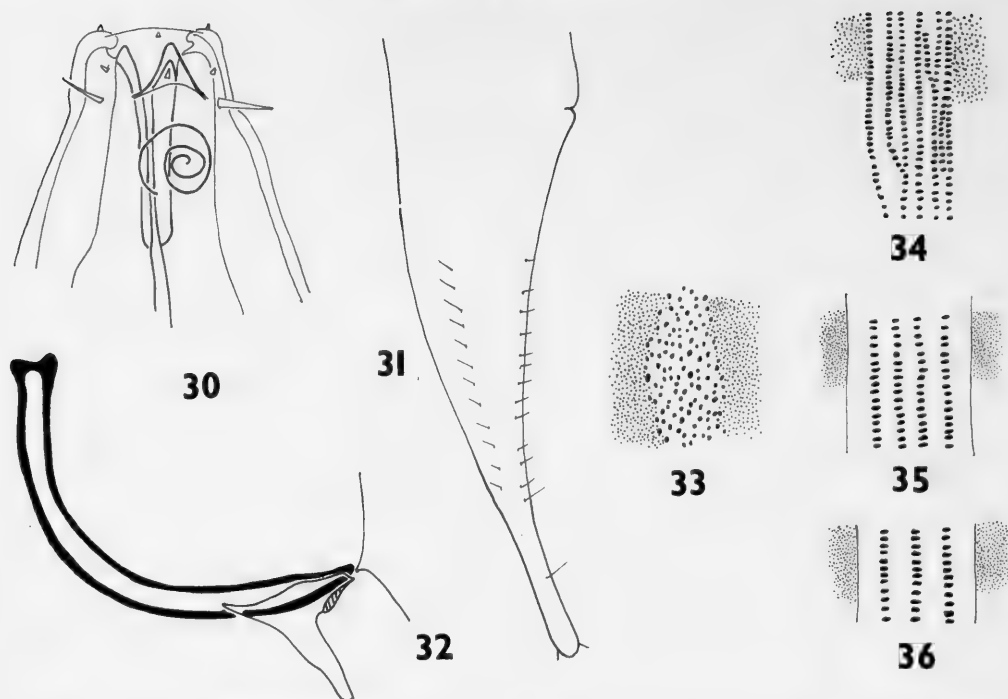
Measurements (in mm. in order of body lengths above)

MALES. Body breadth : 0.16 ; 0.15. Oesophagus length : 0.47 ; 0.49. Head diameter : 0.023 ; 0.024. Diameter of amphid : 0.012 ; 0.014. Distance of anterior edge of amphid from anterior end of body : 0.014 ; 0.011. Length of pharyngeal rods : 0.030 ; 0.030. Excretory pore from anterior end : . . . ; 0.29. Length of cephalic setae : 0.008 ; 0.008. Width of lateral differentiation, at posterior end of oesophagus/middle of body length/level of the cloacal opening : 0.024/0.020/0.025 ; 0.023/0.021/0.026. Tail length : 0.28 ; 0.36. Cloacal diameter : 0.12 ; 0.11. Spicule length : 0.22 ; 0.22. Gubernaculum length (= length of posterior apophysis) : 0.078 ; 0.075.

FEMALE. Body breadth : 0.18. Oesophagus length : 0.49. Head diameter : 0.023. Diameter of amphid : 0.012. Distance of anterior edge of amphid from anterior end of body : 0.013. Length of pharyngeal rods : 0.029. Excretory pore from anterior end : 0.25. Length of cephalic setae : 0.008. Width of lateral differentiation, at posterior end of oesophagus/ middle of body length/level of the cloacal opening : 0.023/0.028/0.025. Tail length : 0.31. Anal diameter : 0.12. Distance of vulva from anterior end : 2.4.

Cuticle

The cuticle is differentiated laterally over most of the length of the body by a clear zone of cuticle down which run three files of irregularly shaped dots (Text-fig. 36). Both dorsal and ventral to this clear zone the cuticle is marked by very small irregularly arranged dots which continue over the dorsal and ventral surfaces. That is, there is no unmodified zone dorsally and ventrally as in *Mesonchium nini* Inglis, 1961. Anteriorly and posteriorly this regular arrangement disappears, the number of files increases first to four (Text-fig. 35) and then, more anteriorly or posteriorly (at the anterior and posterior ends of the body respectively), five or six. Each file then tends to split into two for longer or shorter distances so that, for example, about the middle of the oesophagus there may be as many as seven or eight files of large punctations (Text-fig. 34) although the dominant number about the posterior end of the oesophagus and the level of the anterior ends of the spicules tends to be four. At the extreme anterior end of the body and posterior end of the tail the regular arrangement in files disappears completely by the files dividing irregularly and indefinitely to produce an appearance such as is shown in Text-fig. 33. As the regularity of the differentiation breaks down the unmodified zones



FIGS. 30-36. *Mesonchium janetae* sp. nov. Fig. 30. Ventro-lateral view of head. Fig. 31. Lateral view of male tail. Fig. 32. Detail of spicules and gubernaculum. FIGS. 33-36. Detail of lateral differentiation. Fig. 33. Just posterior to amphids. Fig. 34. About middle of oesophagus. Fig. 35. About posterior end of oesophagus. Fig. 36. Over the major part of the body length.

flanking the differentiation becomes increasingly narrow until they disappear completely and the major markings become smaller. This is exactly what happens in *M. nini* in which the lateral area, including the clear strips, remains roughly the same width down the whole length of the body while the amount of space occupied by the differentiation varies (see discussion below, p. 549). There are two long files of setae running down the body—one file on each side of the zone of differentiation.

Head and Oesophagus

The structure of the head is the same as in *M. nini*. In describing that species I referred to a difference in the sizes of the three teeth at the anterior end of the oesophagus but I am now sure that such a difference does not exist. All three structures are equally well developed. The amphid has two and three quarter spirals.

Males

The spicules are typical of the genus—relatively simple, slightly curved structures with slightly pointed distal ends. The gubernaculum is small with a prominent apophysis (Text-fig. 32). The tail is typical in shape (Text-fig. 31).

Discussion

The genus *Mesonchium* now contains five species : *M. poriferum* Cobb, 1920 (type species) ; *M. nini* Inglis, 1961 ; *M. pellucidum* (Cobb, 1920) ; *M. punctatum* Timm, 1961 and now *M. janetae* sp. nov. They are all very similar in appearance with very few characters which allow their separation other than the spectacular differences in the lateral differentiation, except possibly in the form of the gubernaculum. Cobb's (1920) descriptions of the form of the differentiation in his two species are insufficient to enable the species to be assessed with certainty but they are sufficient to show that *M. janetae* cannot be confused with either. In fact *M. janetae* is unique in the irregular appearance of the lateral differentiation at the anterior end of the body.

NOTE ON THE STRUCTURE OF THE CUTICLE

The effective zone of lateral differentiation in the genus *Mesonchium* is the clear area, not simply the area covered by the large dots (This was the area measured to give the various width measurements for the lateral differentiation given on p. 547.) Now in both *M. janetae* and *M. nini* the width of this zone remains fairly constant while, where the number of files of dots is reduced the size of the dots increases. It appears that the ratio between the area of the dots and the area of cuticle, i.e. lateral differentiation as defined above, surrounding them remains constant. This suggests two things. Firstly, the zone of lateral differentiation is fairly sharply demarcated and is demarcated by factors other than those determining the occurrence of the large dots and secondly that, although the number of dots may be reduced, some factor applies to ensure that they still remain in a balanced relationship with the whole area of lateral differentiation around them. This is not restricted to the genus *Mesonchium*, although it is much more spectacular in this genus than in some others, since a comparable situation occurs in all other genera in which there is lateral differentiation. When the punctations are large the spaces between them are also larger than elsewhere on the body. Elsewhere (Inglis, 1962) I have argued that the modifications of the cuticle in the genus *Euchromadora* are largely restricted to the lateral aspects of the body because only there will they act to strengthen the cuticle while impeding the flexibility of the body by the smallest amount possible and the same argument can be applied to the cuticular modifications found in other chromadoroids, such as *Mesonchium*, *Longicyatholaimus*, *Pomponema* and many other genera of the families Cyatholaimidae, Chromadoridae, and Comesomatidae. This does not, however, explain the necessity for the relationship between the size of the punctations and the area with which they are associated. Wieser (1959) describes the lateral differentiation in a species of *Metacyatholaimus* as "In these longitudinal rows each dot is actually the upper disc of a cuticular dumb-bell-shaped structure that consists of a basal and an upper disc, connected by thin stem". (Wieser, 1959, p. 38. See also Wieser's fig. 36c), and exactly the same shape is shown by the large punctations in *Xyzzors fitzgeraldae* and in *Choniolaimus wieseri*. I would interpret these punctations of the cuticle as canals associated with moulting since their relationship with the area of clear surrounding cuticle

is most easily explained on the assumption that they supply something to the cuticle at some stage or another in the life cycle of the animal.

MONYSTERIDEA

LINHOMOEIDAE

Limhomoeus timmi sp. nov.

Material Studied

1 ♂. Khaki mud at a depth of 54 metres. 32° 05' S./18° 16' E. on 2.7.61. (Ref. No. WCD 94). B.M. (N.H.), Reg. No. 1962. 603.

Ratios			
<i>a</i>	<i>b</i>	<i>c</i>	Body Length (mm.)
166.7	24.2	23.5	7.5

Measurements (in mm.)

Body breadth : 0.045. Oesophagus length : 0.31. Head diameter : 0.018. Length of cephalic setae, long/short : 0.009/0.006. Length of cervical setae : 0.006–0.008. Distance of nerve ring from anterior end of body : 0.177. Distance of excretory pore from anterior end of body : 0.150. Diameter of amphid : 0.013. Distance of anterior edge of amphid from anterior end of body : 0.036. Tail length : 0.32. Cloacal diameter : 0.045. Spicule length : 0.063. Gubernaculum length : 0.039.

Cuticle

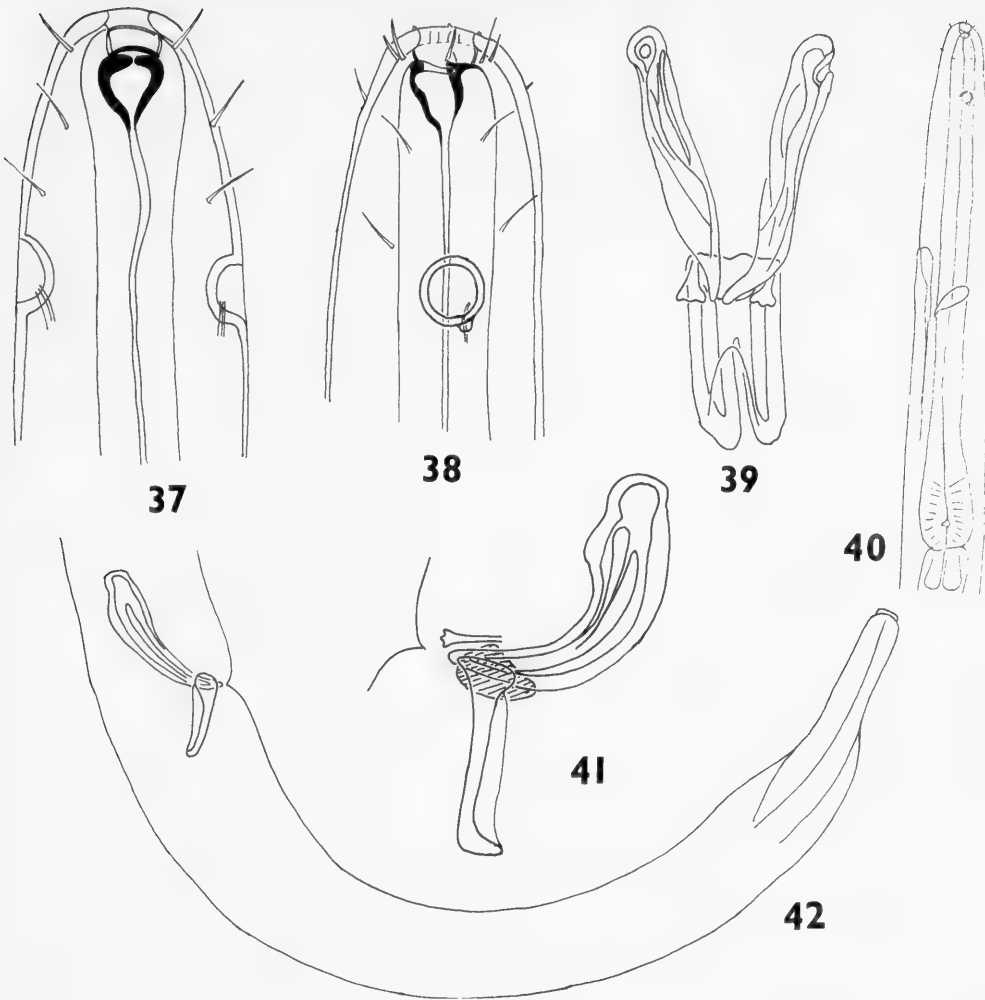
The cuticle is very thin and is marked by very fine, close set striations.

Head and Oesophagus

The head bears six small slightly setose papillae in the inner circle and ten setae in the outer of which six are longer than the remaining four. The anterior end of the oesophagus is modified to form a cavity by the reduction of the ventro-lateral sectors. The walls of the space so formed are composed of thickened cuticle and into the space projects the dorsal sector of the oesophagus as a cuticularized tooth-like structure (Text-figs. 37, 38). There are two circles of six cervical setae. The amphids lie relatively far posteriorly and the amphidial nerve enters them towards the dorsal side (Text-figs. 37, 38, 40). The oesophagus is long and thin with a slight, but distinct, posterior bulb (Text-fig. 40) and a prominent oesophageal-intestinal valve.

Tail and Reproductive Apparatus

The tail is long and narrow remaining roughly the same width along its entire length until just anterior to the posterior end where it narrows rather suddenly to a rounded tip (Text-fig. 42). The spicules are short, stout and elaborate (Text-fig. 41) and the gubernaculum has a distinct apophysis. There are rod-like structures developed from the lateral walls of the cloaca which expand distally to stout three pointed ends (Text-figs. 41, 42). Such structures are figured by de Man (1907) but do not appear to have been reported elsewhere.



FIGS. 37-42. *Linhomoeus timmi* sp. nov. Fig. 37. Dorsal view of head. Fig. 38. Lateral view of head with the dorsal surface to the right. Fig. 39. Ventral view of spicules and gubernaculum. Fig. 40. Oesophagus. Fig. 41. Lateral view of spicules and gubernaculum. Fig. 42. Lateral view of male tail.

Discussion

This species appears to be most similar to *Linhomoeus hirsutus* Bastian, 1865 (as redescribed by Wieser, 1956) and *L. brevicaudatus* (Schuurmans Stekhoven, 1950) but differs in the form of the spicules, the extreme length of the tail and the posterior position of the amphid.

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